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TRANSCRIPT OF LECTURES

SUMMER INSTITUTE IN SYSTEMATICS

at the

SMITHSONIAN INSTITUTION

25 June - 14 July 1967

in conjunction with

AMERICAN SOCIETY OF ZOOLOGISTS

and

SOCIETY OF SYSTEMATIC ZOOLOGY

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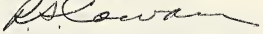
PREFACE TO TRANSCRIPTS

The Smithsonian Institution is pleased to have been host to the 1967 Summer Institute in Systematics. Through the cooperation of granting agencies, professional societies and institutions, we have been able to expose academic systematists engaged in instruction and research in systematic theory and practice to a variety of concepts within the discipline. The mutual exchange of information has been a stimulating experience and has established a strong potential for improving instruction and research in systematic zoology.

We gratefully acknowledge the contributions of the lecturers as well as the participants, the financial support provided by the National Science Foundation and the Air Force Office of Scientific Research and the cooperation of the members of the staff of the Natural History Museum.



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1 April 1968

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BOTANICAL OBSERVERS:

The following attended sessions as invited observers during the week indicated:

26 June - 30 June	Billie L. Turner University of Texas Austin, Texas
3 July - 7 July	Peter C. Raven Stanford University Palo Alto, California
10 July - 14 July	Reed C. Rollins Harvard University Cambridge, Massachusetts

* Transcripts omitted because of various technical problems in recording or because of the informal nature of discussion.

** This transcript was typed by the speaker and is somewhat longer than average.

INTRODUCTION

Ernst Mayr

Museum of Comparative Zoology, Harvard University

The role of systematics in biology--as soon as we use these words, we must ask ourselves just what does the word systematics mean and what does it stand for. This necessitates a bit of an excursion into the history of biology, the history of taxonomy, and gets us right into the philosophy of biology.

It all started with Plato and Aristotle and continued with Linneaus. Now they, the founders of our science, intellectually at least, all saw- or thought they saw- a natural order in the world. They looked for the underlying "universals" which Plato called "eidos" and the scholastics called "essences", and for this reason (because they looked for essences) they are sometimes referred to, particularly by Popper, and the "essentialists". They thought there existed a natural system, and by "natural" they meant something very different from what we mean when we talk about natural systems. They also thought that this natural system was at the same time a system by which one can identify things. They expressed this by presenting classifications in terms of dichotomous keys. There is a great deal of similarity between their ideas and approach in classifying and the prodedures in the field of logic, and it is not at all amazing that Aristotle was, at the same time, the founder of a theory of classification and of Logic.

For as long as animal and plant taxonomy were largely coextensive with zoology and botany, this concept of taxonomy as an identifying science was not fatal. It did become so when physiology and embryology and other branches of biology broke away from zoology and botany. As the new experimental biologist, more and more, began to look at taxonomists as sort of useful citizens that would identify specimens for them, but they thought that taxonomy as such was quite devoid of all intellectual content.

We remember, particularly the older ones of us, this period of time when taxonomy was the absolute bottom of the totem-pole in biology. When I view the contemporary value, I feel that the worst has been over for ten or fifteen years. There have been earlier periods in the history of taxonomy when we had ups and downs. There was the existing period when there was a change from classifications as mere identifying schemes to something very different, namely evolutionary schemes. That came in 1859 with Darwin and the acceptance of the evolutionary theory. This could have been the great turning point in the history of taxonomy, but in a way it, unfortunately, was not because taxonomy was largely used at that time merely as evidence in favor of evolution, and reciprocally, the taxonomists themselves used evolutionary concepts usually for purely internal purposes such as an improvement of classifications in a way that would not contribute particularly to a strengthening of a bridge between taxonomy and other branches of biology.

Unfortunately, some of the greatest contributions made by the taxonomists during this period, for instance, population thinking, which we will come back to presently, the theory of geographic speciation,

and others that I shall mention, were incorporated into biology unnoticeably and so to speak, anonymously, and the taxonomist never got the credit he deserved so richly for these major contributions.

The taxonomist knew that this neglect was unjustified, but he seemed to be trapped in a dead-end road produced by developments in biology. But then, eventually came a second major change--in the 1920's and in the 1930's when there was a change in intellectual climate. One might almost say that is consisted in the rediscovery of the fact that taxonomy is a vital branch of biology.

Now there are several components in this development that are of importance. One of them was that some of the most enlightened leaders of biology, people like Julian Huxley, G. G. Simpson, Bernhard Rensch, and Dobzhansky, all of them discovered how many major contributions taxonomy had made and were using them in their evolutionary and other studies.

There was a second development. Taxonomy to a large extent had been a science of amateurs, and the amateurs had made marvelous contributions. I am the last one to minimize the great achievements of the amateurs. But now in the 1920's, 30's, and 40's, the education of the young taxonomists became far more professional. They were no longer the narrow specialists that they had been, but they acquired and had to acquire, an excellent training in genetics, in statistics, in the study of behavior, in biochemistry, and other branches of experimental and functional biology.

Concurrently with this development, the naturalists also began to assert themselves. No longer was the naturalist satisfied merely to collect specimens to be classified in a museum, or worse still, to classify specimens purchased from commercial collectors, as was done by the wealthy owners of private bird and butterfly collections. The naturalist now insisted on studying taxa as living organisms and pursuing such studies in the field and in the laboratory. This resulted in the general recognition that the universe of the systematist is far greater than was previously envisioned. Taxonomists now took an ever-increasing interest in evolutionary, ecological and behavioral research problems, and indeed, assumed leading roles in these fields.

This new viewpoint is well reflected in Simpson's 1961 definition: "Systematics is the scientific study of the kinds and diversity of organisms and of any and all relationships among them."

If we accept this sweeping definition, which considers systematics the scientific study of the diversity of organisms and all and any relationships among them systematics becomes something more comprehensive than taxonomy.

Until a few years ago, I agreed with those who said, "Well, taxonomy and systematics are just two words for one and the same thing," but on mature reflection, I now agree with Simpson that taxonomy is the science of classification and that systematics, the broader concept is the study of diversity, the study of the relations of living things in thw world.

Why should we define systematics so sweepingly? In order to justify this, let us have a look at biology as a whole. Some years ago, I pointed out that there are basically two biologies: one which deals with functional phenomena and investigates the causality of biological functions and processes; the other one, evolutionary biology, which deals with the historical causality of the existing organic world. Functional biology

takes much of its technique and "fragestellung" from physics and chemistry and is happiest when it can reduce observed biological phenomena to physical-chemical processes. Evolutionary biology, dealing with highly complex systems, operated by historically evolved genetic programs, each of which is unique, must pursue an extremely different strategy of research in order to produce significant results . . . and this is, essentially, the comparative method for which the taxonomist has laid the foundation. Indeed, I can hardly think of an evolutionary problem that is not posed because of some preparatory work of the taxonomist.

Perhaps the most important contribution everymade by the taxonomist, and I never get tired of emphasizing this again and again, is the introduction of population thinking into biology.

Biology, as were all sciences, was permeated until the nineteenth century by typological thinking. When the experimental psychologist speaks of THE rat or THE monkey, or the racist of THE Negro, this is typological thinking. The early Mendelians were pure typologists--a mutation changed THE "wild-type" and the result was a new type of organism--a new species.

This strictly typological thinking dominated the experimental biological literature up to the 1920's and the 1930's. Yet, already in the 1840's and 1850's some zoologists had started to collect large series of individuals, population samples as we would now say, and began to describe variation. In fact, in one of the early instruction booklets of Spencer Baird, made for the collectors of the Smithsonian, he makes this very point--always get a large series because we want to study variability . . . this was around 1862.

Heinke's studies of the variations of the herring populations published in 1898 is an outstanding example of this type of research, and some leading botanists followed his example. A description of the variation both within and between populations not only became a standard component in all taxonomic papers on the better-known groups of animals, but more importantly, it engendered a whole new way of looking at the universe. Up to that time, the typologist following Plato and Aristotle was thinking of the underlying types, the essences, and they thought that this was the really important thing--to use Plato's famous allegory--the visible phenomena were merely like shadows on a cave wall.

To the population thinker on the contrary, the total variability was the real thing and the mean value, the average was merely the abstraction, so it was a complete upside-down turning of the underlying basic philosophy. From taxonomy population thinking spread into adjacent fields. Except for the mathematicians, all founders of population genetics had either been trained in taxonomy or were working in close contact with taxonomists. Population thinking has spread from there into the behavior field, into ecology, and in each individual case the influence of taxonomy or a given taxonomist can be demonstrated. Population cytology as practiced by Michael White and by some botanists is another area where population thinking has been very productive. And it is an approach that is still spreading into other areas of biology.

Population thinking, however, not only led to the establishment of entirely new fields, but it also led to a drastic reconceptualization of some old established fields. Let us, take environmental physiology. It was in part physiologists like Bergmann and Leuckart, in part ecologists

like Semper, but primarily zoological systematists like Gloger, J. A. Allen and Bernhard Rensch, who were responsible for the discovery of adaptive geographic variation and the establishment of the climatic rules. Up to the 1920's the physiologists and geneticists insisted that geographic differences among populations of a species were non-genetic modifications of the phenotype and of no evolutionary interest. The type of the species was not affected, as it was put! But this interpretation changed drastically when Schmidt for fishes, Sumner for Peromyscus, and Goldschmidt for Lymantria proved the genetic basis of adaptive difference between geographic races. It was only then that the physiologists took full cognizance of this most interesting phenomenon. Admittedly, some physiologists find it still difficult to get away from the typological thinking of traditional physiology. The stress on differences between individuals, the recognition of differences between populations, the emphasis on the phenotype as a compromise between multiple selection pressures, all this kind of thinking which has come straight out of evolutionary systematics has exercised - and is continuing to exercise - a profound influence on environmental physiology.

One of the weaknesses of the taxonomists in the past has been that most of them didn't realize what a rich gold-mine they owned. The very area of biology that most deserves to be called biology, because it does not just deal with merely the physical and chemical properties of living materials, depends to a large extent on taxonomy for its raw material, for a clear posing of problems, and most importantly, for most of its conceptualization.

Our more enlightened colleagues in the non-taxonomic branches of biology recognized this sometimes more quickly than have many of the taxonomists. It is the way the taxonomist thinks that has been largely responsible for the development of some newer branches of biology such as population genetics. And in ecology, likewise, we have on one hand a concern with functional problems, such as those dealing with energy flow and energy turn-over in systems, and we have areas in which systematics poses the problems, such as all the problems of diversity, the difference in the richness of faunas and floras in different climatic zones and habitats. In problems of species competition, of niche utilization, and many other problems of modern ecology, it has been a succession of prominent taxonomists who have been the leaders in posing new problems and in advancing them toward solution. And, of course, there is no area of biology in which the taxonomist has played a more important role than in evolutionary biology.

It has often been said that it is not a coincidence that Darwin wrote his Origin of the Species after eight years of concentrated effort in barnacle taxonomy. Julian Huxley, in the introduction to the New Systematics emphasized how much systematics had "become one of the focal points of biology".

Not merely evolutionary theory itself, but the solution of many specific problems, are the contributions of taxonomists. The role of isolation, the mechanism of speciation, the nature of isolating mechanisms, rates of evolution, trends of evolution, the emergence of evolutionary novelties, all of these are topics to which taxonomists, including the paleontologists, have made more significant contributions than other kinds of biologists. It is the taxonomist who encounters the full sweep of evolutionary phenomena and who encoutners them at every level of his research.

At these various levels, the taxonomist is forced to distinguish between non-genetic and genetic variation, he must distinguish between individual variants and different species, and is for various reasons, much concerned with such phenomena as polymorphism. It is the taxonomist more than anyone else, to take up another level, who is forced to study the population structure of species.Terms like "geographic variation," "climatic rules", "isolates", "ecotypes", "secondary hubrid belts", and many other similar words document his interest in the adaptation of populations, in the past history of these populations, and in the dispersal of individuals between populations leading to gene exchange.

On the next higher level, it is the taxonomist who is concerned with the nature and the meaning of species. For--some of our friends notwithstanding, and those of us who were at Ann Arbor know what I am referring to--species do exist. It was field taxonomists who have made the greatest contribution to our understanding of isolating mechanisms and species ecology. Indeed, one might say these taxonomists have been responsible for the development of a separate branch of biology, the science of species, which is just as legitimate a branch of biology as is cytology, the science of cells, and histology, the science of tissue.

To list a few other areas where systematics has played an important role, there is the whole field of biogeography dealing with the distribution patterns in the diversity of life. This field is traditionally to such an extent the domain of the taxonomist that there is no need to argue about his contribution.

Or to take another field, ethology, comparative behavior, here again major contributions were made by taxonomists, or at least by people with taxonimic background and interest. I could go on listing field after field, and the reason I am expressing this and citing such an abundance of examples is that looking at some recently published papers, it is quite evident that some of our younger colleagues are totally unaware of this long history of important contributions made by taxonomy to biological science.

I hope that these discussions have made it clear why I am willing to go along with Simpson and make a distinction between taxonomy, more narrowly defined as the science of classification, and systematics, more broadly defined as the science of organic diversity.

In much of the preceding discussion, I have concentrated on the impact of systematics on biology. I now go back and discuss once more some of the changes within systematics, and I hope I am not anticipating too much what some of the subsequent speakers will be dealing with.

Let me start with a few words about the theory of classification. We have very little in the literature on the theory of classification, a field which is still in the flux -- and what I will present is my own personal interpretation, and I know there will be some people in this audience who will disagree with what I will now say -- and I hope that they will have a better opportunity than I to get this all discussed in the next three weeks.

As I see it, there are basically only three theories of classification; we can designate these as the essentialist, the nominalist, and the evolutionary theory. These three terms indicate extraordinarily different

underlying philosophies, and this does make itself felt in many of the operations and applications. I have already tried to outline what I consider the essentialist approach to classification. It was originally based on the idea that we are dealing with the products of creation. It is essentially a "static" approach (I do not like to use this word because static is often used as a dirty word), because it is not dealing with the evolutionary flux of things. It is an attempt to identify the "nature" of the taxa, or the "essence" of the taxa. It has an identificational tendency; it is usually associated with a neglect of variation because variation is considered only a deviation from the basic "essence" and for this reason it is not interested in the biological study of variation. This is obviously an anti-essentialist characterization, and I hope that if there are any essentialists present they will try to refute the implications of this portrayal in the forthcoming weeks.

The second basic theory of classification is the nominalist one which is based on the idea that only individuals exist (and this is a definite reaction against the essentialist approach), it was founded by Occam, well-known for Occam's Razor, but his real contribution was the establishment of nominalism. This, I am sure, the historians of science will one day find to be far more important than it is considered now because there is a good deal of evidence that the empirical thinking in the philosophy of British science has emerged from this nominalist approach.

According to the nominalists, only individuals exist. There are no such things as universals. We bracket things together and give them names. The operations of our minds make things, they make "species" and "genera" in the philosophical sense. Birds are our creation according to the nominalists. Good taxa are those which our operations group together. The original approach of the numerical pheneticists was typically nominalistic and their insistence on operationalism is very typical for this approach.'

The person who has perhaps most clearly elucidated the difference between the nominalist approach and the evolutionist approach is Simpson with his example of identical twins. He said that there are two ways we can refer to identical twins and their similarity. We can say that Tom and Jack are identical twins because they are so incredibly similar, or we can say that Tom and Jack are so incredibly similar because they are identical twins. Now the nominalist would choose the former way of putting it is saying Tom and Jack are identical twins because they are so similar, shile the evolutionist would say Fom and Jack are the product of a single fertilized egg, and as a result of that, they are so similar that it is by the process of evidence and inference that we arrive at the fact that they are identical twins.

The third theory of classification is the evolutionary one. The thesis of this is that the diversity of the organic world which we see is a product of evolution. Birds, bats and penguins are not the product of our minds, but are the product of evolution; and the task of classification is to "discover" not to "make" the units of evolution. The postulate is made that the descendants of a common ancestor have the greatest genetic similarity and are, therefor, best grouped together. How we then apply this theory has been well-explained by Simpson: what kind of evidence we can use for the inferences that we draw, the laws of probability, the nature of scientific theories--this would take us much too far.

The classification that emerges from our operations is a scientific theory and has all the characteristics of a scientific theory. This is another thing so many taxonomists have overlooked. A classification has explanatory value in terms of explaining how these groups are related and how they are the descendants of common ancestors. It has a predictive quality like any good scientific theory because if our classification is good we can predict the classing of not yet discovered taxa, and if it is a good classification, the utilization of any new kinds of characters, such as biochemical or behavioral characters, should reenforce or merely slightly modify the accepted classification. I have already come to the third characteristic of a scientific theory, it is tentative and is, of course, continually subject to modification as new evidence is found.

This last characteristic is always very upsetting and annoying to our friends who are concerned with information storage with the help of computers because they would like us to adopt once and for all a final and ultimate classification so that we can freeze it into out information storage. But, unfortunately, no theory is ever completely final, and if you ask the physicists they will tell you how far from final even Newton's theories were.

Let me take up another matter because I have quite often been misunderstood on this. We talk quite often about alpha-, beta-, and gamma-taxonomy as if these were three stages that followed each other chronologically just as, let's say, the identification period, and the purely taxonomic period, and the systematics period of taxonomy are historical stages. Or, somebody might say essentialist, nominalist, and evolutionary taxonomy might be stages. It would not be correct to think of alpha-, beta-, and gamma-taxonomy as a sequential replacement series. These three terms cannot be precisely defined. They are sort of a short-hand description of different taxonomic operations.

Usually, by alpha-taxonomy we mean the discrimination of the entities of nature, the description of species, and in some cases, of higher taxa, the clarification of what is merely an individual variant and what is a species...let's just simply say that it is the discrimination of the basic entities to be classified.

Beta-taxonomy mainly deals with putting thsee entities into a scheme of classification, while gamma-taxonomy deals with all the interesting biological findings and generalizations that emerge from our operations at the alpha and beta levels--studies of populations, studies of trends and rates, evolutionary studies of all sorts--all these go in with gamma-taxonomy.

It depends on the group of organisms with which you work, which of the three is the most important. If, for example, you work on mites (acarines), where ninety per cent of the species of the world have not yet been discovered by necessity, what you do is mostly alpha-taxonomy and a certain amount of beta-taxonomy, and probably, very little gamma-taxonomy. If you are in the fortunate position of being an ornithologist you do very little alpha-taxonomy, a certain amount of beta-taxonomy--and you wish that you could do more if you had more characters--and you spend a good part of your time, if not most of it, doing gamma-taxonomy. But it is important to emphasize that this is not a chronological sequence. Even when it comes to a group as well known as the birds, we continue to do alpha taxonomy, we still find new species, new subspecies, we still regroup our genera, and we still discover occasionally, that a species in the literature is nothing but a "morph" of a polymorphic species. I do not know of a single leading gamma taxonomist, including Simpson, who has not done also a great deal of alpha-taxonomy,

even in recent years. Simpson just finished detailed monographs of fossil lemurs of Africa of Patagonian mammals, and I myself, have just done some parts of Peters"s Checklist which is, just alpha-taxonomy.

Now when in 1942, I contrasted Peters"s the old and the new taxonomy, I did not compare alpha-, beta-, and gamma-taxonomy. I contrasted the typological-essentialist approach with the evolutionary-biological type of systematics. And there is a great deal of difference between the two even when you are doing alpha-taxonomy...at least this is how it looks to me.

The typologist is forced by his underlying philosophical assumptions to act as if he were dealing with definite types. He stresses morphotypes and discontinuities. The biological systematist knows that he is dealing with samples of variable populations. He is interested in the biological meaning of this variation. He is interested in the meaning of the taxa he is distinguishing. He knowingly deals with living organisms. He studies all their attributes, including their ecology, behavior, bio-geography and biochemistry. To repeat, all this is equally applicable and equally important at the alpha, beta, and gamma levels of taxonomy. There is no conflict between alpha-taxonomy and the "new systematics".

I don't know whether there is any necessity in saying anything about the "new systematics". I did not coin the word, but for better of for worse, rightly or wrongly, I've been considered by many as the foremost proponent of the "new systematics".

"New Systematics" was a kind of rebellion against typological thinking and against the worst kind of old-fashioned classical taxonomy. It was primarily characterized by two aspect: First, the "back to nature" emphasis-the emphasis on the living organism, its behavior and other characteristics in life; Secondly, the stress on the populational aspects of species and of infraspecific taxa.

Neither of these emphases were new in 1940 or 1942, and as I have said repeatedly in publications, there has always been a "new systematics" from Linnaeus to the present...and I might add that I made this point long before any of my critics. Since the "new systematics" of the 1940's was so importantly concerned with populational aspects I prefer to refer to it now as population systematics. And if currently there is a new systematics, it deals without a doubt with the higher taxa and is what we might call "macro-taxonomy".

I don't know whether I should bore you at all with a few words on nomenclature. I say the word "bore" quite deliberately, and knowingly, because as far as I am concerned there is no more boring subject in all of biology than nomenclature. But since it is important, we just cannot get away from it in taxonomy when we deal with millions of different entities... we must have a set of names in order to refer to them.

Scientific nomenclature is a language, as many authors have pointed out; it is a sytem of communication; is is a system of information storage and retrieval. And any such communications sytem, and it does not matter whether it is inside biology or outside biology, in linguistics or technology, any such system is founded on three basic principles. The first one is that it must have unambiguity (uniqueness). When I use the word "stair" I have to make it quite clear that I am referring to a part of a staircase rather than looking intently at a certain person (stare). "Stair" has to

be properly defined. Unambiguity is one of the three basic principles of nomenclature.

Universality is another principle. The more people use a language--and this is our major gripe about the Russians...they don't speak English--the more useful a system of communication is. And fortunately, very fortunately, and this is one of the developments that came out of the Strickland Code...in fact, it goes all the way back to Linnaeus...in zoology we have only one language, a single form of communication, the international zoological nomenclature!

The third of these important principles is that of stability. Once a name is in use for a certain thing we should never use another name for the same thing, lest we damage the information retrieval value for the system. We can't call the thing one day a pencil and another day an inkpot...this would confuse everything. Alas, there are far too many taxonomists who change names at the drop of a hat.

Now it is important to remember that these are the three basic principles of any system of communication. All other so-called laws or principles of nomenclature are only secondary; they are only methods in helping to achieve appreciation of these three basic principles-they are executive methods. Now if things are all that easy, why do we have so much trouble? Mostly because the three principles themsllves are often in conflict with each other. It would lead me much too far afield to say more about nomenclature except that it has become quite obvious that the sequence of importance of these primary priniples may be quite different in nature and in immature branches of taxonomy.

Let me now come to the end. Any one who knows the history of biology in the last fifty years knows how much better the value of systematics is appreciated now than it was a decade or two ago. Anybody who every tried to get a grant in taxonomy twenty or thirty years ago knows that. I remember two luncheons I had with Warren Weaver, then with the Rockefeller Foundation, trying to make him set aside some money for systematics. He was very friendly, but made it clear that they just didn't give any money for that sort of thing. Now that things have really changed for the better, it is up to the taxonomist to strengthen and accelerate this trend. He who treats taxonomy as a kind of stamp collecting, he who is more interested in the names of organisms than in the organism itself, he who fails to recognize the exciting biological problems which his own taxonomic findings raise, in short, he who treats taxonmmy as if it were a purely clerical occupation rather than a branch of the biological sciences, will only add water to the mill of those who downgrade taxonomy. We others, and I think we are now in the vast majority, consider systematics one of the most important and indispensable, one of the most active and lively, and one of the most rewarding branches of biological science. For there are few other subjects that teach us as much about the world we live in than the study of the diversity of life--in other words, systematics.

HIGH SPEED COMPUTATION IN SYSTEMATICS: A DEMONSTRATION

James E. Mosimann

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This presentation will take the form of a demonstration of the Smithsonian Institution's time sharing computer consoles. A major portion of the presentation will consist of your using the consoles yourselves to obtain answers. This "hands on" approach will permit you to directly evaluate the utility of such a system in your own work. It is to be stressed that the major purpose of this presentation is the actual use of the computer.

The brief talk which we now give will serve as background for the demonstration. For those of you who are unfamiliar with computers some notes will be helpful. There is nothing novel in these notes, and they are only intended to provide a setting against which your experience with a time-sharing system can be better understood.

The notion of physical aids for computation is an ancient one - as witness the abacus. In a sophisticated form, the notion of a calculating machine antedates the publication of "the Origin of Species". Long prior to 1859, Charles Babbage, a Cambridge mathematician and founder of the Royal Astronomical Society had proposed his "analytic engine" which was to be controlled by punched cards.

But the history of electronic computers is much more recent. During World War II, IBM engineers under the direction of Howard Aiken, a Harvard professor, completed the first computer, called Mark I. This computer was not a purely electronic device, but used electro-mechanical devices like relays. The first large purely electronic computer was ENIAC ("Electronic Numerical Integrator and calculator") which was completed at the University of Pennsylvania in 1946. Two people, J. W. Mauchly, a mathematician, and J. P. Eckert, an engineer, were instrumental in its development. A company formed by these two professors was bought out by Remington Rand Inc. in 1950. Then in 1951, Remington-Rand marketed the first commercially available computer, UNIVAC I. This computer was a direct descendent of ENIAC. (It is interesing to note that the first commercially available computer was not from IBM. Their first commercial computer, the IBM 701, was available for delivery at the end of 1952.)

In order for the IBM 701, UNIVAC I or other machines which appeared in the early fifties to accomplish a given task the computer had to be told what to do; that is, programmed. In the early 1950's this was a tedious task which required many detailed instructions. Programming was essentially limited to experts, programming specialists. However, in 1954 a project was started in connection with the IBM 700 series of computers which has had a revolutionary effect on the scientific use of computers. This was the development of FORTRAN (FORmula TRANslation) in large part due to J. W. Backus of IBM. Technical details were first publisehd in 1959 by P. B. Sheridan. Programming manuals were available before this date. From the point of view of the systematist this is the most important single development of this brief history. FORTRAN permits a scientist who is not a computer specialist to do his own programming. For example, one can write a statement like

Z = X/Y.

This sort of statement is readily understandable. It tells the computer to take the number that is stored in some location X, divide it by the number that is stored in location Y and to store the answer in location Z. A FORTRAN statement is translated by the computer into machine language. Using FORTRAN one can write instructions in a form moderately like english and mathematics and have the result understood by a computer.

A computer cannot stand alone. It is part of an overall "system". We can consider the system aspect by analogy with a simple desk-calculator system. For example, one may be computing a mean using some calculator like a Friden or Monroe. The data must be entered into the calculator (INPUT). Then following decisions made by the operator calculations are performed (DATA PROCESSING). Finally an answer is obtained and transcribed from a register to paper (OUTPUT). The time to perform all three functions is important: Input time, Data Processing time, Output time. If any one time is prolonged unduly, the result is the same in that the answer is delayed. The total time for input to output can be called THRUPUT time.

INPUT	DATA PROCESSING	OUTPUT
Input via Keyboard from pencil data copy →	Processed by mechanical accumulator →	Output on register Transcribed to paper
	↑ direct Control by human operation	

The same model can apply to a much more sophisticated system.

INPUT	DATA PROCESSING	OUTPUT
Input via punched cards, tape, keyboard →	Processed electronically →	Typewriter, line printer, cards, visual display
	↑ indirect control by program	

The concept of THRUPUT time is as valid as before and using this notion we can distinguish between two broad classes of data processing. In "Information Processing," the data processing itself is often relatively simple, but masses of data must be handled and INPUT and OUTPUT times account for most of the THRUPUT time. In "Scientific Processing", INPUT and OUTPUT times are relatively short and the data processing itself tends to be complicated, and data processing time accounts for most of the THRUPUT time.

(A) INFORMATION PROCESSING: INPUT-processing-OUTPUT

(B) SCIENTIFIC PROCESSING: input-PROCESSING-output.

Both types of data processing are important in systematic work. For example, information retrieval in which one would attempt to find out "how many Plethodon cinereus are in the collection from Ontario and Quebec" would fall into type (A). Here the computer would scan a list for certain code numbers representing the animals in question and for other codes representing the localities. An example of (B) would be the calculation of a correlation coefficient of Height and Width in a small sample of Chrysemys picta. In general, the problems faced in developing efficient systems for the two kinds of data processing are quite different. Today we shall discuss and demonstrate (B) only. Most of the data processing of an individual scientific problem falls into this category.

At this point we can take as an example a simple computer system. (1) There is a central processing unit, or CPU. This processor performs the mathematical and logical work (2) There is a memory unit intimately connected with the CPU, the size of which will vary with individual systems. Here there is the capacity to store information. The processor will access information from the memory, act upon it, and transmit new information to the memory for storage. (3) There is some means for input of information. Typically, it might be a paper tape reader, which is slow, a card reader which is faster or a magnetic tape which is still faster. In any event, information must be put in an acceptable form before the system can receive it. (4) There is some means of output. Paper tape, typewriter, or line printer produce the answers.

If the memory is sufficiently large, one can store in it a set of instructions which is called a "compiler". These instructions enable the computer to translate FORTRAN input into machine language instructions. As we have noted FORTRAN is a language which is reasonably close to English and common mathematical notation. Using a FORTRAN compiler, the machine takes over the job of machine language coding.

In a typical system a programmer will submit his "source' deck to the computer operator. The deck is then read into the computer. The computer "compiles" the FORTRAN program into machine language. Data is read in and processed. If there is a program error the program must be changed and the process repeated.

The development of FORTRAN was a major step in making computers accessible to the working scientist. Another step is more recent. This is the development of "Time Sharing and Multicple Access Computing (MAC)" (cf. Hackman, 1966). Here a number of different persons in widely scattered areas have access to the same computer by teletype or other means. Thus an individual scientist has direct access to a large computer. This is the type of system which the Smithsonian is using for stored program processing and which we shall use today.

What we shall use is a teletype and dataphone. The teletype information which we shall input through a keyboard or punched tape is in digital binary form. This information is translated into a tone which is transmitted by a regular telephone line to another dataphone at the computer, in this case on River Road, Bethesda, Maryland. There is a communications computer, a GE DATANET 30 which is designed to work in real time as well as apare time. (By 'real time" is meant that the computer handles requests instanteously). The communications computer then transmits information for storage in a memory unit, a magnetic disc called a DS-20. Another computer comprises the central processing unit

or CPU. This is a GE-235 computer and has direct communication with both the DATANET 30 and the DS-20 memory.

When using the teletype, one is in communication with the DATANET 30. Very little time is spent using the CPU or GE-235. When the command RUN is typed, the GE-235 accesses the area of the memory in which your program is stored. It will then compile the program, run it with your data, and the answers are returned to you at your teletype.

Your programs in this system will be written in BASIC, a language similar to FORTRAN. You have already received a BASIC manual so you are probably somewhat familiar with the characteristics of this language. An important point to note is that your program is stored in the DS-20 in BASIC, in program form. Each time the command RUN is given your program is recompiled and then run. Hence it is a simple matter to make changes in the program. In fact, using BASIC one can change one line of the program at a time. This is an important feature of this system. At this point, before proceeding with the demonstration we can consider a simple BASIC program to add two numbers:

```
10      READ      X,Y
20      LET       Z=X+Y
30      PRINT     "Z="Z
100     DATA      35.6, 23.1
999     END
```

Here the first statement which is numbered 10 is a READ statement. The computer is to read a number and store it in location X. It is also to read another number and store it in location Y. This is done as follows. The computer looks for the first DATA statement. (Here number 100.) The first number in this statement, 35.6, is put into X; the second, 23.1, is stored in Y.

After the READ statement is a LET statement, LET Z = X+Y. The computer then adds the number stored in X to the number stored in Y and stores the result (58.7) in location Z. Thus Z contains the answer. (Incidentally X still contains 35.6, and Y, 23.1.) The next statement PRINT tells the computer to print the answer. The portion within quotes is a label. Whatever is inside the quotes will be printed as written. The Z outside the quotes gives the location whose number is to be printed. Thus the computer would print

```
Z = 58.7
```

and the answer is obtained. If we had written statement 30 simply as

```
30 PRINT Z,
```

The answer would not be labeled and would look like

```
58.7
```

The statement END is necessary to tell the GE-235 when to stop compiling. The end statement must have the highest statement number in the program.

One of the programs which will be demonstrated is A Key to the Genera of Ecuadorian Snakes written by Dr. James A. Peters. The central

concept involved in this program is a branching concept. We can illustrate this concept here. Suppose that somewhere in a program we find statements like

```
...   ....

184     IF I 175 THEN 187

185     PRINT  "LYSTROPHIS"

186     STOP

187     PRINT  "TRIMORPHODON"

199     STOP

...    ...
```

Here I is a location into which the number of ventral scales of a snake has been read. In Statement 184, the computer compares this number with 175. If it is greater than 175, the computer proceeds to statement 187, prints

TRIMORPHODON

and then proceeds to statement 188, STOP, and stops. On the other hand if the number stored in I is less than or equal to 175, the computer simply goes to the next statement in sequence. This is 185 PRINT "LYSTROPHIS". The computer then prints this name, proceeds to 186 STOP and stops. In this way, once having arrived at statement 184, the computer identifies a snake with more than 175 ventral scales as Trimorphodon and one with 175 or less ventral scales as Lystrophis.

A program to compute a mean is simple to write in BASIC. Suppose one has a sample of N numbers. A typical program is

```
10          DIM     X     ( 100 )

20         READ     N

30         LET S = 0

40         FOR I = 1 TO N

50         READ X ( I )

60         LET S = S + X ( I )

70         NEXT I

80         LET M = S/N

90         PRINT "MEAN =" M

200        DATA 3, 2, 1, 3

900        END
```

This program contains several kinds of statements which are important. We can examine it statement by statement.

The first statement 10 DIM X (100) is a "dimension" statement. It reserves 100 storage locations identified as X(1), X(2), X(3),..., X(100). This places an upper limit of 100 on the sample size which the program can handle.

The next statement reads N, the number in the sample. In this example N = 3, the first number in statement 200 DATA ... . The next statement 30 LET S =), stores a zero in location S. This is called "initializing". It assures us that initially S contains a zero. The next set of statements 40 to 70 is important. Since the number in location N is 3, statement 40 is effectively

40 FOR I = 1 TO 3.

The statements following 40 up to 70 will be repeated with I = 1 then I = 2, then I = 3. With I = 1, statement 50 becomes

50 READ X(I).

The number READ is the second number in statement 200, namely 2 and 60 becomes

LET S = S + X (I) .

This latter statement says add the number in X(I) to that in S and store the result in S. We remember that initially S contains zero. Hence X(I) is added to zero and stored in S. S now contains X(I). The next statement is NEXT I which sends us back to the FOR statement in 40. Now I is set equal to 2. Proceeding through the "loop" again we have this time

50 READ X (2)

60 LET S = S + X(2) .

Thus X(2) is read (in this case the third number in statement 200, X(2) = 1.) Then X(2) is added to S and the sum stored in S. But this time S already contains X(1) so that what is stored in S is X(1) + X(2). We then proceed to 70 NEXT I which sends us back to statement 40 where the process is repeated with X(3) in statements 50 and 60. The result is that after going through the loop 3 times, S contains the sum of the numbers X(1) + X(2) +X(3). This third time upon encountering NEXT I, I = 3 and we pass to the next statement. In 80 the sum is divided by N and stored in M. M is then printed in 90 to give the mean.

All the concepts illustrated will be discussed in the demonstration. At this point we can begin our computer demonstration. We shall demonstrate programs for computing means, standard deviations, correlation coefficients, eigenvalues and eigenvectors, and for keying Ecuadorian snakes among others. Each participant also will operate the console.

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NUMERICAL TAXONOMY

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Systematics today is full of excitement and activity. It is abundantly clear to anyone familiar with current developments that taxonomy is undergoing a period of rapid conceptual and procedural change probably unequaled since the immediate post-Darwinian era. Numerous publications in journals such as Systematic Zoology, Evolution and Taxon reflect the effervescence of ideas which has suddenly enlivened this field. The last great era of scientific progress in systematic biology came in the 1930's with the so-called "new systematics." There is little doubt that the consequences of the present developments will be even more fundamental as regards theory and especially practice.

There are three main reasons for the changes in the philosophy and methodology of systematics of the past decade. These are (1) a growing dissatisfactoon with the logical and conceptual bases of contemporary taxonomic theory and methodology; (2) continued pressure from new material and new data needing to be incorporated into the taxonomic system; and (3) the advent of the electronic computer as a generally available scientific tool.

Although taxonomists communicate their results voluminously, they generally do not communicate the methods by which these results are obtained, making it difficult for others to interpret the validity and significance of their findings. Taxonomic prodedure is generally an automatic and subconscious assessment of similarities, based on characters weighted a priori or during classification, and involving phylogenetic speculation and intuition.

Tremendous stresses are being placed on the existing system because of the vast amount of new information about biological material which is becoming abailable. Data of value in taxonomy accrete at an an ever-increasing rate. It becomes ever more obvious that the procedures of the present systematics are unable to digest and process this information. The challenge of new information comes from three sources: new organisms, new characters, and new detail in both characters and organisms.

The speed, power and general availability of electronic digital computers has vastly increased in the last few years. There are now few universities in the world laying claim to being major national and international research centers that are not equipped with at least one of these machines. One of the reasons why the earlier work in numerical taxonomy was not taken up by systematists was that, however sound the ideas that accompanied it, the computations necessary for establishing classifications on a numerical basis were impractical because of their volume. This situation has drastically changed. Almost every biologist who wishes to can have access to a digital computer, and the numerous uses to which such machines have been put in the biological sciences (in addition to the field of systematics) are evident from the published literature. In short, we might say that numerical taxonomy developedin part because the technology

for doing the numerous computations necessary in this work developed along with it. It is important to stress that much of taxonomy is procedure and one of the main reasons why this discipline is currently facing a revolution (or even 'explosion'; Simpson, 1965) is because so much in taxonomy is procedure concerned with data accumulation, and subsequent processing and retrieval of information.

Before proceeding further, we need to understand clearly the meaning of three terms. Classification is the ordering of organisms into groups on the basis of their relationships by descent or similarity, or by both. Taxonomy is the science of classification involving both the theory and practice of classification. Systematics may be considered as the scientific study of organic diversity, including the descrpption of the organisms, their history and phylogeny, when known, and the study of the evolutionary mechanisms bringing about such diversity. It is therefore the more inclusive of these terms. These definitions are fairly generally accepted among zoologists and many botanists in the United States and elsewhere (e.g., see Simpson, 1961).

Sokal and Camin (1965) have distinguished three approaches to the analysis of taxonomic data. They are operational, empirical, and numerical taxonomy, and their importance is considered to be in that order. In operational taxonomy statements and hypotheses about nature must be subject to meaningful qusstions, i.e., those that can be tested by observation and experiment. Empirical taxonomy is based on many observed and recorded characters, taxa being grouped according to a majority of shared characters (Simpson, 1961; Sokal, 1962). The method by which the number of shared characters is determined varies with the empirical school. Empiricism may or may not be quantitative. Numerical taxonomy has been defined as ". . . the numerical evaluation of the affinity or similarity between taxonomic units and the ordering of these units into taxa on the basis of their affinities. The term may include the drawing of phylogenetic inferences from the data by statistical or other mathematical methods to the extent to which this should prove possible" (Sokal and Sneath, 1963:48). Thus, numerical taxonomy as originally defined includes computation of similarities among taxa and description and analysis of taxonomic structure as well as attempts at reconstructing branching sequences in evolution by numerical techniques such as those of Camin and Sokal (1965). Numerical taxonomy as generally practiced is both operational and empirical.

Fundamental to the establishment of any taxonomy is the decision on whether taxa are to be monothetic or polythetic (Beckner, 1959; Sneath, 1962). A monothetic group is defined by the possession of a unique set of features, and classification on monothetic principles is a series of successive logical divisions into ever smaller subsets sharing one or more states of a character. By contrast, a polythetic classification places together organisms that have the greatest number of shared features. No single feature is either essential to group membership or is sufficient to make an organism a member of this group.

The more inclusive usage of "taxonomic relationship" comprises relationship on any basis, be this phenetic, phyletic, cladistic, genetic, etc. To specify which type is meant, one uses an adjective restricting the meaning, as in "phenetic relationship," "cladistic relationship," etc. Phenetic relationship has been defined as ". . . arrangement by overall similarity, based on all available characters

without any weighting. . . . " (Cain and Harrison, 1960:3), ". . . without any implication as to their relationship by ancestry" (Sokal and Sneath, 1963:3). These definitions imply exhaustive estimates of similarity among phenotypes. There may be different phenetic relationships based on characteristics of different developmental stages or organ systems. Whether these diverse aspects of phenetic relationship estimate the same fundamental parameter is still an open question, pursuit of which may lead to the study of similarity of genetic fine structure (Michener and Sokal, 1966). The magnitude of phenetic relationships estimated in numerical taxonomy depends on the kinds of characters and similarity coefficients employed (Sokal and Michener, 1967). For a measurement of phenetic relationships, the principle of operational homology must be employed. A phylogenetic concept of homology will lead to unwarranted conclusions (Sokal, 1962; Hull, 1967) because under such assumptions homology cannot be defined without recourse to phylogenetic reasoning, and yet phylogenetic reasoning is based on taxonomy and morphology, which in turn is based on homology. Operational homology is fundamentally empirical. Two characters are operationally homologous if they are very much alike in general and in particular (Sokal and Sneath, 1963:70). Phyletic relationships, unlike those that are phenetic, cannot be decomposed into additive components. We can only say that most phylogenists have usually considered at least three elements in expressing phylogenetic relationships. These have been phenetics, cladistics, and time relationships, which we may call chronistics. By cladistics, is meant a study of the pathways of evolution, i.e., how many branches are there, which branch came off from which other branch and in what sequence? If we wish to speak of cladistic affinity, following Cain and Harrison (1960), we would have to develop some measure of expressing this.

Natural classifications. The aim of taxonomy has been to establish "natural" taxa. This term has assumed different meanings depending on the philosophical school of taxonomy employing it. In the first half of this century "natural" in a classification has largely meant grouping into monophyletic taxa, essentially according to cladistic concepts. Such classifications have been and are difficult of achievement, and most purported natural, phylogenetic classifications have in fact been phenetic, more or less natural classifications. The numerical taxonomists, following Gilmour (1961), propose to base classifications as those yielding taxa whose members are more phenetically similar to one another than they are to members of other taxa. It follows from this concept of naturalness, that a natural taxon will be most predictive.

The central concept of the phenetic school of taxonomy is the measurement of phenetic similarity. Some definitions are necessary before we can discuss this subject. We define taxon as meaning a taxonomic group or class of any nature and rank. Operational taxonomic units (OTU's) are the lowest ranking taxa in a given study. These may be individuals, or races, species, or genera. They are the basic units that are to be grouped into higher ranking taxa. A character is a property or feature which varies from one OTU to another. It is coded into distinguishable states. Thus, amount of hair on a leaf is a character. Slight, medium and heavy may be the three states in which this character occurs among the OTU's to be classffied. We must also distinguish between taxa (plural of taxon) and categories.

Taxa are actual groupings of OTU's observed in nature, regardless of the basis on which the grouping has been done. They are allocated to categories which are the formal hierarchic levels in a classificatory scheme. Thus, Homo sapiens, carnivores or mammals are taxa, while species, genera or families are categories.

The nature and measurement of similarity is really one of the fundamental problems of taxonomy regardless of whether the approach is phenetic, cladistic or some philosophy in between these. The problem of the nature of similarity transcends that of biological taxonomy. Although it is an ancient philosophical problem, it has recently become acute in a variety of fields because of the introduction of automata for classification and identification.

Similarities in numerical taxonomy are computed on the basis of many characters, often as many as 100 and in some cases several hundred. One as yet unpublished study was based on over one thousand characters. All kinds of characters (morphological, physiological, cytological, etc.) are equivalent. This principle is generally accepted by systematists of most schools of thought. Taxonomic equivalence of all kinds of characters leads directly to the absence of weighting of any character, which can be defended on numerous genetic and logical grounds. It can be seeen most clearly when we attempt to construct an objective criterion for weighting characters.

The numerically coded data are arrayed in a so-called data matrix which is a rectangular matrix whose t columns are the t operational taxonomic units (the OTU's whose similarity is to be measured) and whose n rows are the n characters on the basis of which the similarity is estimated. The values in the matrix are the states X_{ij}, representing the character state value of character i for OTU_j. Since the character states are often in different scales which would unequally weight the coefficients, they are frequently standardized by some technique.

Three types of coefficients have been employed in the computation of similarities or affinities. The first and simplest are the so-called coefficients of association. These employ largely, but not necessarily, those characters subdivided into only two character states or attributes, which are frequent in microbiology. A second method of computing similarities is based on Pearson product-moment correlation coefficients between various taxa (Sokal and Michener, 1958). In this method (and for the coefficient of taxonomic distance) the characters are free to include an arbitrary number of characters state classes and can be entirely continuous. Correlation coefficients vary from -1 to +1. A third method determines the dissimilarity between two taxa as the distance in an n-dimensional space whose coordinates are the characters (Sokal, 1961). The distance can be calculated by a simple formula from analytical geometry. Once similarities between each pair of OTU's have been computed, they are arrayed in a $t \times t$ matrix of similarity coefficient between all pairs of OTU's. This symmetrical similarity matrix serves as the fundamental imput for all subsequent clustering procedures, i.e., for attempts at structuring the taxonomic units into a system.

One of the most important areas in which new work is being done and where new problems have arisen is character selection. It was

early recognized that phenetic classifications based on few characters are unreliable. It therefore is important to know how many and what kind of characters should be employed. Numerical taxonomy started with a viewpoint that might be called fundamentally genetic, to the effect that any sample of characters should represent the genotype equally well. The hypothesis of nonspecificity, as proposed by Sokal and Sneath (1963), asuumes that there are no distinct large classes of genes affecting exclusively or principally one life history stage, such as larvae or adults, or one class of characters from special regions of the organism, such as head, skeleton or leaves. Evidence accumulated to date indicates that the nonspecificity hypothesis is only partly valid. Among reasons deduced for the failure of the nonspecificity hypothesis to hold completely is the possibility that the effects of a large proportion of the genes are limited to a single life history stage, sex or body region. Thus, character samples from any one stage, sex or region would not suffice for estimates of overall phenetic relationships. Yet there would be a sufficient number of genes with measurable effects in all stages, sexes or regions being compared so that the resulting classifications would not be entirely independent. Such a explanation seems reasonable to us in view of our present knowledge of developmental genetics.

Results from the nonspecificity studies as well as from another study, in which independent investigators reclassified identical sets of objects (Sokal, Michener and Rohlf, 1967b), have led to the recognition of what Rohlf and Sokal (1967) have called the "uncertainty principle in taxonomy." This simply states that it is impossible to reclassify independently the same set of organisms by conventional or numerical means and obtain results comparable beyond a certain degree of replicability. Our experience in this field has not yet been sufficient to indicate between which bounds this uncertainty may lie.

The underlying assumption for the establishment of a phenetic classification is that the OTU's are not regularly spaced throughout phenetic space (character space) but that regions of higher and lower density occur, i.e., that there are clouds of OTU's in a phenetic hyperspace (a space of four or more dimensions) with more or less distinct gaps between them. The nested hierarchy is the predominant and formal mode of biological classification. It is a powerful and esthetically pleasing method of achieving ecomomy of memory. It rests upon the general belief of branches within branches promulgated by the cladistic or phylogenetic school (the universality of this phenomenon, especially at the lower ranks, remains to be demonstrated). However, as we shall point out later, only certain types of distributions of similarities among OTU's in phenetic hyperspace are amenable to being hierarchically clustered. Research in numerical taxonomy has already demonstrated that the phenetic similarities of some groups are not satisfactorily represented by clusters within clusters. Much work remains to be done in the comparative study of distributions of similarity coefficients in various taxonomic groups. Similarities in such distribution patterns may occur among groups quite diverse from the point of view of conventional taxonomy. It is, for example, quite likely, but not necessarily so, that parthenogenetic organisms will have phenetic relations distinctively different from those of sexually reproducing organisms.

The three main clustering methods employed in biology have been described as linkage methods by Sokal and Sneath (1963). In all of these methods the criterion for joining is gradually lowered from an initial high similarity value in which all OTU's are represented by a disjoint partition (single OTU in each subset) to low similarity values at which the classification is represented by a conjoint partition (all OTU's are in the same set or taxon). Single linkage, described by Sneath (1957b), permits a single linkage between an OTU and a cluster or between members of two clusters to establish a new, more inclusive cluster. While two clusters may be linked on the basis of a single bond, many of the members of the two clusters may be quite far removed from each other. Clustering by complete linkage requires that a given OTU, or a cluster, joining another cluster at a certain similarity coefficient S_i must have relations at or above that level with every member of the cluster to be joined. This yields compact and conservative clusters compared to the long, strung-out groups of single linkage. The average linkage method calculates average similarities of clusters with prospective joiners and since its intial development by Sokal and Michener (1958), classifications based on it and on its various modifications (Rohlf, 1963; Proctor, 1966) have demonstrated higher cophenetic correlations (see below) with the original similarity coefficients than classifications based on other clustering methods.

The results of a numerical classification are usually represented by means of a phenogram, a dendritic arrangement or dendrogram of the OTU's based on phenetic relationships. These diagrams indicate along one axis the similarity between OTU's or stems bearing more than one OTU. Phenon lines at right angles to the similarity axis enclose all OTU's born by one stem into a higher ranking taxon. The positions of phenon lines are arbitrary and do not necessarily correspond to any of the formal categorical levels. Because phenograms collapse multidimensional relationships into a single phenetic dimension, there is appreciable distortion of the original relations given in the similarity matrix.

To avoid the distortions necessary by the two-dimensional nature of phenograms, numerical taxonomists have recently experimented with other means of representation of taxonomic relationships. Among the most popular is the three-dimensional perspectives.

A major unresolved problem of cluster analysis in biology is the fact that few, if any, clustering methods have been devised which do not bias the resulting classification in the direction implied by the clustering procedure. It is, therefore, of considerable importance to try to establish general clustering procedures whose algorithm would vary depending on the scatter and distribution of the OTU's to be clustered. Such self-adjusting programs are still not extensively developed, but it seems to me that we shall not be representing nature faithfully, nor learn much about the forces that have resulted in the phenetic patterns being observed, unless we produce programs of this sort.

In the early days of numerical taxonomy, the success of a numerical classification was generally judged by its similarity to a classification established by conventional means. As the subject developed, there seemed no inherent reason why the traditional,

partly intuitive, classifications should be considered as the final arbiters, and attempts were made to develop internally sufficient criteria for the goodness of a classification. Two main approaches have been followed. Sokal and Rohlf (1962) have used the method of cophenetic correlation which consists of correlating the original similarity matrix with so-called cophenetic values, which are the values of similarity implied by the structure of a given classificatory phenogram. The goodness of a classification can be measured as magnitude of the correlation between a phenogram and the original similarity matrix. Rubin (1966) has approached the subject from the general point of view of establishing a stability function for a given classification, which is to be a measure of the homogeneity within groups and the inhomogeneity among groups at a given hierarchic level. Once such a function can be defined, one obviously wishes to maximize it, that is, one wishes to arrange the OTU's to be classified in such a way that the function becomes maximized.

Since the ultimate operational taxonomic units are individuals and since it is obviously not feasible to classify all or even many individuals of a population, samples of these individuals have to be taken. The exemplar method of Sokal and Sneath (1963) is intended to cut through this Gordian knot. Exemplars are representatives of supposed OTU's to be classified. Even single exemplars are considered representative if the taxonomic relations being investigated are of sufficiently high categorical level so that the differences of interest are presumably greater than the differences among the individuals within the cluster being sampled.

Along with the recognition that phenetic similarity should form the basis of a general classification has come a renewed emphasis on operational cladistic approaches. Camin and Sokal (1965) use discontinuous characters or characters coded into separate states. Three hypotheses are made about the characters. (1) That characters are unique, by which is meant that the ancestral state arose only once in the taxa at hand. (2) That we have knowledge of the direction of the evolutionary trend, i.e., we know which state is derived and which is primitive. (3) That evolution is not reversible, i.e.,having reached state 3 of character X, we cannot return to state 2. It is known that these are not valid assumptions for all cases, although they are probably true for the majority of characters and taxa. Inconsistencies in these assumptions are, however, frequently revealed by the method itself. The technique finds a solution which gives the most parsimonious arrangement of the branches of the tree in terms of the number of evolutionary steps which need to be taken to arrive at the phenetic pattern exhibited by the taxa studied. A computer program has been developed (Bartcher, 1966) which solves for these by an iterative procedure and constructs a cladogram, a tree of branching sequences. By these methods and others undoubtedly under development, it appears possible, that evolutionary lineages will be traced analytically by means of computers.

Biological taxonomy will be affected by the computer revolution in ways other than through the development of numerical taxonomy. Automatic data processing will revolutionize the storage and retrieval of taxonomic information for museams and catalogs (Sokal and Sneath, 1966). The approaches of numerical taxonomy have already done much to de-emphasize the often legalistic and sterile aspects of naming

organisms. Nomenclatural reform is clearly on its way. It is likely that developments in automatic data processing will rapidly relegate problems of nomenclature to the position of relative unimportance they merit. Some of the birth pains of automation will be felt in taxonomy as in other fields and traditionally minded workers will presumably resist the changes. The controversy about numerical taxonomy will doubtless continue for some time to come until a new, "synthetic" theory of taxonomy, accepting what is sound from various schools, becomes established. The revolution the computer has wrought in taxonomy has only just begun.

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Discussion

VOICE: I was wondering if you are suggesting that objectivity rests in two people being able to run the same computer and get the same answer?

SPEAKER: Objectivity gives you absolutely no guarantee of correctness. We may both be objectively wrong. If you and I can first of all agree what characteristics are of an object that you wish to classify, and if we can then agree on given measures of similarity, then I can look over your data and say that you have or have not arrived at a classification that has the criteria of goodness of a classification which I think are desirable.

VOICE: You seem then to shift whatever may or may not be homology to correspondence; what do you mean by correspondence?

SPEAKER: If I can make the same statement about two things. For instance, I could say that the chair and the table have legs. In analogous structures I can, for instance, make a series of corresponding statements about the wings of birds and insects. There are a number of statements about the aerodynamics of the wing that I could make and which would match what was said about the bird and the insect. But by any fair consideration of overall similarity, taking all characters on which one could possibly compare these structures, they would agree only slightly.

VOICE: You say that different similarity coefficients will give you different relationships, and yet the numerical systematist must code his characters. But isn't that a kind of a priori weighting, when you do code the characters; and you claim to get around that.

SPEAKER: What we would like to do and approach but have not yet done totally satisfactorily is to try to code them into fundamental logical statements, possibly into yes-no statements, so that one can get the information into binary units.

VOICE: Sometimes we see characters that seem to be highly correlated with the environment. Now can you reduce that to a reasonable measurement?

SPEAKER: It depends on what it is that you are measuring. If you are describing the genotype of the organism only, then you probably want to discount that. If you are measuring what the organism is like in nature, then you want to measure phenetics as you did. It is the phenetics of the organism that natural selection works on. There are genetic consequences because there are genes behind the phenetics. I think there is much to be learned from a phenetic approach that has relevance to evolutionary and ecological theory.

VOICE: I have been troubled about this species concept. It seems to me that a lot of our concept of species comes from studies of the so-called higher forms, vertebrates and higher plants. Do you think a lot of our difficulty comes from the fact that this is so, and if the

species concept was looked at in a broader context then we might have some modification that would be acceptable.

SPEAKER: This gets me back to comparative phenetics. I agree with you, that there are many different kinds of species. I don't wish to claim that our way of looking at this is the way, I don't think that there is one way, but I would submit that interesting insights are going to be learned in comparing, for instance, what has been called a species in birds with what has been called a species in insects. And there is the problem of asexual species. This is where phenetics can really make a contribution, and this is one of the challenges to come.

VOICE: Is the species Homo sapiens an example of a good species? What does it grade into, what does it change into; it's not confluent with any other fusing population.

SPEAKER: Possibly, suppose that you did study the human species,not knowing any of the things that we do about their biology. Phenetically, you might come out with a variety of groups. Phenetically, the sub-species may become species.

VOICE: How do you taxonomists handle species which are extremely variable, such as dogs?

SPEAKER: That depends on what it is that you are doing. If you are going to make a study of the systematics of species then you will take an individual from one species and another. This is really only a problem if you are tied to the biosystematical definition of a species. How can you correspond phenetic diversity with genetic unity? What you will have is a series of individuals. Would you suppose that if you took twenty individuals from the different breeds of dogs, that wolves would come closer to certain of the dogs than to some of the fancy breeds?

DISCUSSANT

Stanwyn G. Shetler
United States National Museum

I think that it should be said at the beginning that numerical taxonomy has really brought computers to taxonomy, and if they had not done it in the name of numerical taxonomy, someone else would have. One of the more disquieting aspects of this is that this revolution has challenged not only our methods but our logic. The problem is a theoretical one, and a methodological one, and I will remark about both aspects.

In theoretical, we think of numerical taxonomy basically as the phenetic classification. In the early days of numerical taxonomy there was a fundamental confusion of the historic aims of classification. I feel that this has not been completely upset yet. The goodness of a classification in the sense of an identification scheme is certainly to be goverened purely by phenetic repeatability or predictability. When it comes to the goodness of a classification in the sense of a phylogenetic arrangement, this becomes the function of evolutionary development or evolutionary reality which we cannot measure. This can only be inferred from biology and paleontology. And at this point it becomes important to know, for example, whether it is polyploidy, aplomixis, inbreeding or outbreeding, and applied phenetics in a pure sense at this point becomes hazardous and mechanical. Thus, I think that every classification has been and must be a part in theoretical construct. And this can be a construct based on sort of subjective weighing or theorizing, or it can be the arbitrary mathematics of numerical taxonomy.

I see numerical taxonomy as only a new typology, in which arbitrary computational means are used to establish clustering. The new typology is illustrated quite will by this idea of an exemplar.

Now, a few remarks about numerical taxonomy as a method, which we may call operationalism. I think that it must be operational to sense in which communication can be very complex, and in a practical or functional sense in which communication must be simple. So the goodness of a classification can be judged by the degree by which the successful taxonomist appears to have resolved these two demends of operationalism for his classification, a theoretical demand and a practical demand. Operationalism is a function of more things. It is a function more than objectivity. It is a function of efficiency, as well as repeatability. When you measure the numerical approaches against this criterion, the conventional ones measure up fairly well if we were to look at it in terms of the input and output approach.

I don't think that taxonomy has to be operational, in the practical sense, to have great value. The reality is in the construct, not in the subspecies.

This brings up my final point, I think that numerical taxonomy is largely built around the notion of discrete units in nature or binomial variations, situations where you can make a binary decision between yes or no. When you deal with populations in nature, especially with racial variations, you have to deal with parameters, and the statistics of those parameters.

I will summarize by saying three things. I think that numerical taxonomy has made an enormous contribution by introducing statistical reasoning. It has brought a new mathematical appreciation of relativity of taxonomy, it has put in mathematical terms what the practical taxonomists have known for a long time. And finally, I think that the numerical taxonomist finds its chief utility in the quantification of this pattern of clustering, and it has its least utility in its interpretation of the theoretical dimension of classification.

INFRAGENERIC GROUPINGS

Dean Amadon

American Museum of Natural History

Below the genus, only three systematic categories are in general use and provided for in the International Rules of Zoological Nomenclature. These are the subgenus, the species, and the subspecies. The first of these, the subgenus, is not regarded as very important by most systematists. Furthermore, it is best discussed in connection with the genus. Hence we shall give it no further mention here. Paleontologists, because of the nature of their work often haev to think in the terms of the genus rather than the species.

This leaves the species and the subspecies. I also wish to include a category known as the superspecies, although it does not yet have the usage it deserves.

The species is the only taxonomic category that can be defined in precise restrictive terms, rather than in general relative ones. That is, if we omit the individual organism which isn't mormally thought of as a taxonomic category. The definition reads about as follows: "A species is a freely interbreeding population whose members do not interbreed with those of other populations". In other words, it is a reproductively isolated population. The fifty individuals of the Whooping Crane and the two or three hundred Orang-utans are examples of species. They don't interbreed with other cranes or apes. and if they did, would probably either be sterile or produce sterile hybrids like the mule.

The so-called higher categories, genus and above, are, on the other hand, subjective and must be defined in relative terms. It is a fact that there is a group of trees known as oaks, whose relationship is evident and which may be conviently grouped in a genus Quercus. Hence we may define the genus as a group of related species. But some species, e.g. the ghinko tree, seem to have no close living relatives at all. We have to leave this species in a genus of its own, a monotypic genus, and even in a monotypic family and perhaps order. There are many such monotypic genera; scores or even hundreds are recognized among birds alone, and there are only 9000 species of birds. At the present, scores of monotypic genera are recognized. Furthermore, there is great difference of opinion as to how closely a group of species must be related to be included in the same genus. Linnaeus used much more inclusive genera than are customary today. On the other hand, some "genus splitters" approach the point of having a genus name for every species, which destroys the value of this category. But this is subjective.

The subjective quality applies to all higher categories. There is as much or more difference of opinion as regards the limits of families, orders, and classes, as of genera.

To return to the precies, in most cases there is no difficulty about recognizing one, at least as long as we stay in one place and consider only the present time. To be sure, we do have some puzzlers. This is sometimes due to the fact that two perfectly good species are difficult to tell apart bt comparing them. Species this similar are infrequent among birds, though they occur, but are commoner in insects.

A classic case is Drosophila pseudoobscura and D. persimilis, two intersterile species, so similar they can be separated morphologically only by slight statistical differences in measurements. Such extremely similar sympatric species are known as "sibling species". This is not a very good name because it implies that, like human siblings, they are more closely related to each other than they are to other species. This is not necessarily the case. Two sibling species may be less closely related genetically, or ecologically, than are ones superficially much less alike. Conversely, genetic differences even much below the species level may be as visible as day and night, for example, in color phases or other morphs.

We encounter other difficulties in discriminating between species. In the final analysis, they stem from the fact, first convincingly demonstrated by Darwin, that species are not fixed, immutable creations, but rather dynamic, evolving populations that inevitably change with time and which often split into two or more daughter species in somewhat the same way that an amoeba divides into two. Even when a species does not subdivide, it changes, as just noted, with the passage of millenia. Of the latter type of change I shall say but a word. If we could follow any species back far enough in time, eventually the gap between ancestor and descendant would be greater than that found within the limits of any species today. Just how long "back far enough" may be varies tremendously. Many species have evolved, we believe, in less than one million years, yet, judging from fossils, some gaps have changed little in tens of hundreds of millions of years. Just where to draw the line in fossil geneologies are regards species is obviously an arbitrary decision. In most cases the geological record is so interrupted and fragmentary that the question is an academic one; in fact, the paleontologist often must work with genera more than with species. It is hardly necessary to add that many species have become extinct, leaving no close relatives.

Taxonomy seems to be somewhat like theoretical physics-there are a few constants and many relatives. We may mention one other constant. In the study of evolutionary systematics and phylogenies we are dealing with an actual history. If we could reconstruct every living individual organism all the way back to the primordial ooze, we would have a perfect history of life and its evolution on earth. Or relatively perfect, for we still would not know everything about even one of the trillions of individuals. But this will never be done even in the roughest outline. G. G. Simpson estimates that there were 15 million generations in the ancestry of the horse alone. It is worthwhile bearing in mind, however, that phyletic taxonomy represents an attempt to trace a dramatic evolutionary geneology that was enacted down to the last species, subspecies, and individual.

Viewed in this chronological or geological way, the species as a category may seem to disappear- it marges imperceptibly with what went before. Perhaps, however, this is to look at matters the wrong way. A species, as we have said, is a population of interbreeding living organisms. From this point of view, there are at any moment of time a certain number of species. But of Tyrannosaurus rex abd even the extinct Passenger Pigeon we should assert not that they are but that they were species. We may then conclude that of the species occurring 100 years ago or 100,000 years ago, such and such were ancestors of, or identical with such and such species of the present moment. Further, we need not go.

The taxonomist who works with living forms must usually infer

species status from morphology. The paleontologist must always do so, and usually from very fragmentary material. So fragmentary, in fact, that he often cannot be sure whether he has before him remains of a single species or of several allied ones. But since the paleontologist has the only direct evidence of the course of evolution during 99.99 per cent of its duration, he is heard with respect, however scanty his evidence. And if he is obliged often to speak in terms of genera rather than species, we may be sure that it was individual organisms grouped into species that enacted the history he relates to us.

Species not only change in time, they may subdivide into one or more daughter species. This process involves space as well as time. It is responsible for the existing proliferation of species, and it is best studied in contemporary forms. As noted above, we have little difficulty with most species so long as we restrict ourselves to one locality here and now, e.g., the District of Columbia in 1967. If we begin to trace species spatially, we sometimes run into problems. The common Song Sparrow is a rather different looking bird by the time we reach the coast of Alaska. The population of the Aleutians is made up of birds perhaps three times the weight of the eastern Song Sparrows, and of a duskier hue of plumage. Are they the same species? In general, the answer is "yes" if a more or less continuous series of intermediate interbreeding populations exist, as they do in this case. Gene interchange can then occur, and a favorable mutation arising in one area can spread throughout the range of the species. In a few cases it has been shown that the geographical extremes in such complexes are genetically incompatible. A well known example is provided by the meadow frog, Rana pipiens. Prof. John Moore showed that as one proceeds from New England to Mexico along the extensive distribution of this frog, various adaptations occur, often correlated with changes in climate. The two extremes are now so divergent that, as shown by laboratory crossing, they are virtually inter-sterile. This is one criticism of species, but since gene interchange throughout the chain is possible, it is customary, though in some respects arbitrary, to say that only one species is involved. So long as such communication exists it is even possible that the extremes might again become genetically compatible. If the range were cut in the middle, as so often happens in the long run because of geological or meteorological changes, the two terminal populations would soon, no doubt, become completely self-contained species incapable of exchanging genes with any others.

With rare exceptions, however, if two populations are sterile or produce sterile offspring, we may be sure that they are specifically distinct. The horse and the donkey are species; they will mate but a sterile mule is the result. In nature, we may be sure, there would be strong selection for horses that prefer horses and donkeys that prefer donkeys! Those that could not tell kith and kin would leave no offspring and, further, would produce strong, healthy, long-lived mules to compete with their parents for food.

But though sterility(almost) always proves specific status, the reverse is not true. Many perfectly good species are interfertile. The answer to this conundrum is that if two populations do not interbreed under normal conditions in nature, they are separate species. They have reached the level of distinctness that insures that each will go its own separate evolutionary way from that time forth, forever, or until extinction. One oft-mentioned case is that of the Mallard and Pintail Duck. They are obviously species, and they occur together in thousands over the entire northern hemisphere. Hybrids are almost unknown in nature.

But if we place a mixed pair of these ducks in a zoo, they will mate, produce young, and the young are fertile. The answer is that in the wild these two species, and many others like them, are kept apart by certain isolating mechanisms peculiar to each, in this case certain calls and courtship patterns. In the absence of a mate of the same species in captivity these isolating mechanisms break down.

The kinds of isolating mechanisms are attuned to the sensory equipment of the species concerned. A moth, for example, may recognize its mate by odor; a mosquito by the pitch of the hum produced by the wings of the female of the species. In other cases, isolating mechanisms may be more mechanical, one species of salmon spawning in the spring, another in the fall, and so forth. In plants isolating mechanisms must all be of this nature rather than behavioral. Either plants are cross-sterile or they flower at different seasons; or the pollination is so achieved that there is little or no chance for cross-pollination between related species. (The adaptations preventing self-pollination are more elaborate and have received more attention.)

It is easy to see how isolating mechanisms can be improved by selection between interacting species, as suggested above for the donkey and the horse. But it is very difficult to see how isolated populations can arise within a freely interbreeding population because difference will be swamped out. Therefore one concludes that species in sexually reproducing organisms evolve under circumstances such that the population distinctions cannot be swamped out, that is to say, in physical isolation. We mentioned the Orang-utan above as an unquestionable example of a species. In one sense it is a poor example, since there are two completely isolated populations; one in Borneo, the other on Sumatra. These populations have been separated for as long as these two islands have been separated from each other and from the mainland(where this beast once also occurred, as known from sub-fossil remains). Just how long this is we do not know, but it is a matter of tens of hundreds of thousands of years.

Although the orangs of Borneo and Sumatra are very similar, we may be sure that if they could be bred in captivity as readily and rapidly as fruit flies, it would be possible to demonstrate various genetic differences between the two populations. We may go further and say that if these two populations were isolated long enough, they will become specifically and eventually generically distinct.

It may be noted that the rate at which isolated populations differentiate reflects the selective milieu, and this in turn reflects the inconstancy or constancy of the environment-both the physical and the biotic environment. Some prolific insects have remained very stable over tens or hundreds of millions of years. On the other hand, the proboscideans- elephants and allies- evolved rapidly during the Tertiary, notwithstanding their long generations and low birth rate. Darwin seemed to think also that even domestic animals will evolve or change rapidly, producing many varieties, if they have sufficiently intense selective pressure.

A species may be broken up into two isolated populations in two ways: either the physical environment "moves", as in the case of the orang-utan, because of changes in sea level, spread of deserts, etc., or individuals of the species itself move; these straggle, fly, swim, walk, or are blown to isolated habitats. Such events may be rare, but there is an eternity of time.

Once isolated, the rate at which a population diverges depens on many factors. Most important, as hinted above, is the extent to which the new environment is unlike the old, just so long as it is not so strange that the species is unable to live there at all. Size of population, genetic constitution of the founders, especially when few in number, and other factors play a part.

As a result of this process of geographical speciation, one often finds isolated populations that give every appearance of having formerly belonged to the same species and yet are now so distinct as to be, beyond much doubt, species. Such assemblages of formerly conspecific allopatric species were called superspecies by Mayr and by Rensch, and the species which comprise them may be called allospecies. The concept is a very useful one in evolutionary and biogeographical studies. I have suggested(Amadon, 1966) the use of brackets to designate such superspecies in nomenclature.

The frequent occurrence in the same area, that is, sympatrically, of numbers of related congeneric species shows that even if, as we believe, species always or nearly always evolve as geographical isolates, they later do in hundreds of cases acquire overlapping ranges. So far as the mechanics are concerned, it is the reverse of the original isolating process. Either the environment changes, for example, Sumatra and Borneo again become joined, or the creatures themselves cross distributional barriers. Once they do came together, if they are to survive and become sympatric species, two things are necessary:

1. They must, when separated, have acquired isolating mechanisms which keep them interbreeding, at least to an extent that threatens to swamp out their differences.

2. They must have acquired sufficient ecological distinctions to enable them to coexist. As Gause argued and demonstrated, two species with identical requirements cannot coexist in the same area. This is true in practice even though one might quibble about it philosophically. In practice two species would never be identical in requirements and in reproductive potential(as might, for example, two color phases or eye colors in a single species.) Hence if two species are too similar in their requirements, one will exclude or exterminate the other. This is apparently one of the commonest happenings in evolution.

A population cannot, of course, acquire isolating mechanisms or ecological requirements that are directly adapted to enable it later to coexist with species with which it is not then in contact. Hence speciation must occur <u>in vacuo</u> and is, in one sense, an "accidental" process; but, as we have seen, such accidents are inevitable in isolated populations given suffucient time. The more unlike the habitats of two isolated populations are, the faster will be such drift.

Nevertheless, when two former allospecies come together for the first time, they may still compete to an extent that threatens their survival and/or interbreed to an extent that weakens their genetic integrity. Selection will then quickly act, as suggested above for the horse and mule, to increase the gap in their requirements and to make their isolating mechanisms more effective. To emphasize the radically different conditions that exist before and after two isolated populations become sympatric, one might offer the following tabulation:

1. Allopatric(Isolated) Populations: Chance Evolution of

A. Potential Isolating Mechanisms

B. Potential Ecological Distinctions

2. Sympatric(Overlapping) Species: Adaptive Perfection of

A. Operative Isolating Mechanisms

B. Operative Ecological Distinctions

One may add the following points:

1. Some populations may be isolated so long that even when the resultant species first come together, they may be completely isolated reproductively and so distinct ecologically as not to compete with each other.

2. While we are here concerned with the type of adaptive differentiation that enables closely allied species to become sympatric, it must be remembered that distantly allied forms may also compete, e.g., rabbits and antelopes. This may indirectly hasten speciation.

3. The opposite side of the coin "isolating mechanisms" is "species recognition mechanisms." Even in a species living among distantly related ones, there will be very precise adaptations to insure reproduction, which in animals involves recognition of other individuals of the same species by one sensory mechanism or another. Thus potential isolating mechanisms evolve.

These questions of how isolated populations acquire differences and how these differences interact and are sharpened following overlap of range are, at the very root, not only of speciation but also of efforts to understand the dynamics of the ecological community. It is an active frontier of research and one that must be studied in the field, though with much assistance from the cages of the population geneticist. In a group of islands, such as Hawaii, the largest island is much more varied, ecologically. It has the larger number of species.

Question 1: Voice; Must a superspecies be allopatric?
Answer; I think they should be essentially allopatric; by that I mean one that occurs on land masses(continuous).

Question 2: Voice; Do you consider Meadowlarks to be a superspecies?
Answer; In general once you get that degree of overlap it is best not to use that term.

Question 3: Voice; You haven't said anything about species groups. Comment please.
Answer; It is the next step upward above superspecies, and involves dealing with a monophyletic group and many difficulties. Once one gets above species, everything is to the convenience of the systematist.

The Subspecies Question- About the turn of the century it began to be evident in the better known groups of animals that hundreds of taxa which were described and listed as species have not really achieved that status. For many of them it was shown that where their ranges meet, free interbreeding and intergradation take place. Such forms are not reproductively isolated, and even with the essentially morphological definition

of the species then in vogue, it was obvious to biologically oriented systematists that they could not be species. In other cases, taxa not in contact were nevertheless so similar that it was all but certain that they are not species, even though many of them had been described as such in the early enthusiasm of naming anf classifying. For example, the lions inhabiting a restricted area in India have, in isolation, become a little different from those in Africa. But are they a different species? Surely most would agree in saying "no."

A solution to this dilemma which embodied both practical and theoretical advantages was to formalize the category known as the subspecies. Taxa which have acquired recognizable characters, but which nevertheless can be demonstrated or are assumed to be below specific status were called subspecies, and names were applied to them under provisions introduced into the International Code of Nomenclature. Thus, if the Indian Lion had been described as a species Felis persecus, it became a subspecies of the lion usually associated with Africa, namely Felis leo persecus. Names were available already for many subspecies; they had been described as species.

In the intervening years this concept of polytypic species subspecies has gained wide acceptance, and is now almost universally used in work with the better known groups, such as birds and mammals. In less well known forms, such as insects, knowledge is just reaching the point where this concept can be usefully applied. This polytypic species concept represented an immense step forward. For example, one highly variable South Pacific bird, Pachycephala pectoralis, which occurs on many islands, is now treated as having eighty-odd subspecies. Only after we had associated all of them in a single species could we study this assemblage properly, especially in relation to other true, genetically isolated, species of the same genus.

The polytypic species concept also had a very salutary influence on the genus concept. There is far less excuse for undue genus-splitting after we have reached our taxa, so far as possible, to bona fide units fitting a "biological" species concept. Furthermore, the polytypic species concept, as Mayr so brilliantly expounded in his 1942 book Systematics and the Origin of Species, presented us with a variety of demonstrations that speciation in sexually reproducing organisms ordinarily if not invariably takes place as a result of spatial(geographical) isolation of parts of a former species.

It is often true in science that concepts of the greatest value must later be modified or even discarded. At the present time there is considerable criticism of the subspecies concept. With one practical aspect of this criticism one must express a certain amount of sympathy. The purely nomenclatural aspects of classification have never achieved the acceptance and stability once hoped for. This is partly because of the historical aspects of nomenclature, particularly as embodied in the so-called Law of Priority. We are certainly all willing and indeed eager to give due credit to pioneers in our science. But I think the day is past when we should change a well known name bestowed on a species or subspecies by John Doe in 1810, merely because someone shows that Fred Doe described the same species under a different name ten days earlier. I have suggested(Systematic Zoology, 1966), as have others before me, that all names of valid species and even subspecies should be determined by committees of specialists and then listed in Nomina Conservanda, thenceforth to be exempt from the vagaries of purely nomenclatural change. Of course, there would still be occasional changes, e.g., if

someone proves that the Luna Moth is only a morph of the Cecropia Moth, we would lose one species. Further, there is no reason why subspecies names should continue to have nomenclatorial equality with species names as first proposed by Dr, I. Morph(Systematic Zoology, 1966) and later by me(op.cit.). By such a step a vast amount of name changing could at once be eliminated.

Why there is so much opposition to such measures is puzzling. I wonder whether those in opposition to the fifty year rule which implements Nomina Conservanda have really considered the fact that other biologists may in desperation adopt really retrogressive alternatives, e.g., by using common or vernacular names for species, as some plant ecologists and amateur or semi-amateur ornithologists are already doing.

There are unfortunately scientific as well as practical aspects to the problem of achieving stability in the names of genera, species, and subspecies. Genera, which I have discussed elsewhere(Systematic Zoology, 1966), are not in the scope of today's session. As regards species and subspecies, it is, in literally hundreds and thousands of cases, impossible to know whether a particular taxon is a species or a subspecies. The Indian Lion may, after all, be a species. If we find that it interbreeds with fertility with the African Lion in a zoo, this does not prove that the two taxa are conspecific. We need to know if there are isolating mechanisms in nature and that we shall never know in this or thousands of other cases involving more or less completely isolated taxa. Even dumping out a few African Lions in the range of the Indian one won't do; it would be an artificial situation, in some ways analogous to that in a zoo. The only effective answer would be a change in climate and a halting of human abuse of the land in the Middle East that would enable the two taxa to come together naturally. Then we could see what happens. Fortunately, there are easier cases to study.

Hence it is necessary to be arbitrary. It won't do to treat all completely isolated taxa as species. This was tried and failed long ago. Even with forms whose ranges do meet, there is every stage of interaction from smooth clines in one character(e.g.. Bald Eagles gradually get a little larger as one goes north from Florida to Alaska) to ones that hybridize only rarely and are almost surely past the point of no return on the path to becoming separate species.

Also, we now realize that all isolated or semi-isolated populations are different. Usually if we examine them carefully enough, we can find at least slight average morphological distinctions; or if not, in those amenable to laboratory analysis one can demonstrate genetic and cytological differences(see, e.g., Dobzhansky's work on various western U. S. populations of Drosophila).

Surely one cannot name every such slight population as a subspecies; attempts to do just that have led to a reaction and to suggestions that the entire subspecies concept in the formal sense of naming them be abandoned. Some have suggested that variation should simply be described in geographical terms without use of subspecific names. However, in a species with great variation, especially on many islands, to describe the variation each time is out of the question; merely to list the subspecies and their ranges does call attention to the extent of the variation. Further, under an informal system we lose the international currency represented by Latinized scientific names.

I am not enough of a prophet to know the ultimate fate of subspecies

and their terminology. I suspect, however, that the advantages outweigh the disadvantages, but that only well differentiated populations will be admitted, that is, ones so distinct that they must be recognized in one way or another-either as races or as species. As Selander has stated, to list such a form as a subspecies represents a considered taxonomic opinion as to its rank, and is as such useful. It may or may not in the long run prove useful to indicate in some other manner less well differentiated populations, as done by Vaurie, for example, by the use of asterisks.

So long, however, as we continue to name geographical isolates of very uneven degress of distinctness, it is of some value to indicate ones that seem to be approaching specific status. One way of doing this is by the use of parentheses. For example, Circus(cyaneus) hudsonius would mean that we treat the form hudsonius (which happens to be the American Marsh Hawk) as a race of cyaneus(a related Eurasian hawk), but wish to indicate that the two seem to be approaching the specific level of distinctness.

Populations at this level of distinctness have been variously called "semispecies"(in one sense of the word) and incipent species(but all segregated populations are, in the long run, incipent species and emergent). Perhaps "semispecies is best, in the sense of populations halfway towards species, but it must not then be used for populations believed to be species.

Quantitative Methods- From the above it is evident that species are biological and behavioral entities- self-contained, interbreeding populations that do not cross with other populations(species). Furthermore, that there is no correlation between attainment of species status and degree of morphological distinctness may not use probability. Some perfectly good species are virtually identical morphologically; other very distinct populations are not species. One may also call attention to the tremendous morphological differences that are often found between different sex and age stages of the same species, e.g., the larva and the imago of a butterfly.

It follows that there is no such thing as a "species character" in any general sense of the term. In this respect species are like the abstractions we know as "higher categories". Afetr we have concluded that a population is a species, we can then tell how it differs from other species, but with no assurance that similar characters will define other species.

These properties of the "biological species" as Mayr called it are worth emphasizing, even though in practice the taxonomist often(if a paleontologist, always) must work with purely morphological characters. He knows nothing about the reproductive potential of the organisms he is studying except what can be inferred. He infers that if, after eliminating characters seemingly associated with sex, age, season, etc., a suite of specimens seem to be all similar to each other and dissimilar to others, they probably comprise a species(or, in some cases, subspecies). The "art" of the taxonomist consists in the skill with which he can use what he has learned about some species to help evaluate less well known or new species.

To do this he uses, so far as possible, quantitative methods. As with so many other fields of science, indeed more so, decisions and conclusions often are a matter of probability. Probability involves statistics. One of the new tool of the biometrician is the computer. Some

taxonomists, enamored of this new tool, have concluded that they are ushering in a new era and have dubbed themselves "numerical taxonomists."

But the only species we can be sure of are living species that we can demonstrate to be self-contained genetic entities. From this point on everything is inference. The computer can help us make inferences, but no more than that, We have to learn by some other means that caterpillars are young moths and that a lioness is a female lion.

The Species in Relation to the Total Biological Spectrum- Great and spectacular advances have been made in biology in the past ten or fifteen years. The genetic code has been cracked; the nature and function of DNA and RNA discovered. Molecular biology is quite understandably the order of the day, and it does not much matter whether the molecules come from a horse or from a horse chestnut, for one triumph of molecular biology is the demonstration that the genetic code is pretty much the same in all living things.

This does not mean, as some would seem to imply, that activity should slow down or halt in all other branches of biology. The complexity of the protein molecule is so great as to permit endless variation and evolution. Not only do species differ but even individuals, as made familiar by the problems involved in tissue and organ transplants, blood transfusions, and so forth.

The structure, behavior, and ecology of the hundreds of thousands of new species now living represent the end products of millions of years of interaction and adaptation. The molecular biologist can tell us what makes this possible, but he could never predict from his laboratory that the bio-chemical processes he has discovered would produce after a couple of billion years a man, a redwood tree, or a seventeen-year cicada.

A comparison with the physical sciences is possibly worthwhile. Today the most active field of research is nuclear physics, and specifically investigation of the kinds and properties of ultimate particles. States from coast to coast vie for the privilege of having a new half billion dollar particle accelerator. But could a nuclear physicist reared in isolation and neither shown nor told about the "starry firmament" predict the actual universe as known to the astronomer and cosmologist, even in roughest outline, from his knowledge of nuclear physics? Assuredly not. It is doubtful, in fact, if he could predict that particles united in certain ways will produce a gas known as oxygen, in another way as hydrogen; and that when combined in a certain manner, these two gases will form a liquid that is good to drink!

I think we may then conclude that those concerned with the evolution, activities, and significance of species, including Homo sapiens, need have no inferiority complex. They may turn to the molecular biologist to learn what makes their subjects tick, and hope that he will turn to them to learn what wonders DNA has wrought after two and a half billion years of natural selection in a changing world. In behavior, in ecology, and in some branches of physiology, sound, comparable conclusions are only possible when the specific identity of the material or populations under study is known.

DISCUSSANT

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I think the viewpoint and how we approach a subject is important, referring to what we owrk with and what our background is. Many times we get into semantic arguments and come to dead ends because we are just starting from different points. What you start from often determines what you end up with.

In the species concept, I think we can start at two levels. One is the theoretical level and the other is the practical level. It depends on what group you work with. If you are working with an asexual group does the species concept apply the same way as if you are working with a sexual group? Bacteriologists that I have talked to do not believe in species. In fact, Simpson and Pitterdrigh recognize this, if I acn just give a quote from them. "It is one of the facts of life that an exact definition of a species applicable without question to all sorts of organisms is inherently impossible." And therefore I insist that we have these two concepts theoretical and practical.

Biological species with the interbreeding concept has its limitations. Mainly, that we must be able to define these naturally. And if we put them together in the same situation, it is not natural anymore; somewhat different forms interbreed. Now are they subspecies or species?

We find different forms interbreeding. Within a species there is a greater interchange with a greater amount of fertility among these offspring. Between species we have a great amount of hybridization. I was amazed that there are several books out on this subject. If interbreeding is decidedly less common than breeding within one, or if hybrids are distinctly less fertile than the offspring of parents of the same species, then this is important. There is probably no absolute distinction between populations of one species that interbreed more frequently and produce more fertile offspring and separate species that interbreed less freely and produce less fertile offspring. If this goes to the extreme of no interbreeding, we will have no trouble, but we will have trouble in intergrading, so where will we cut this off? Even inherent in determination of interbreeding is that one individual of a population taken for crossing with one of another, both are representative of their respective species. We are really using morphology to say that the remainder of species would also interbreed or not interbreed due to morphological similarity, taking morphological data and inferring genetic relationships to test this with one or a few individuals. This means we must be aware of the assumption which we have made.

What we can really say is that a species will reproduce more readily with itself and produce a higher percentage of fertile offspring, which is not a clear-cut definition. In this type of thing we would get into some type of probability series, and with probability series based on a large amounts of data we come to statistics. I would not agree with some of the people that we have become slaves to the machine. The machine can only do what we want it to do. We still have to formulate the questions. Sokel's work isn't based on probability.

In geology, we have many breaks, where the record makes it for us. Most species are represented by morphological breaks. In this regard, I would take a strong objection to Dr. Amadon's remark: "Furthermore, there is no correlation between attaining the species status and degree of morphological distinctness. No correlation, I think, is a very strong statement here. We have some species in which there may not necessarily be any, but not all. And as to the remark that species are not usable in geology, I think they are very usable. We have evidence that many of these have living relatives today, and it is mostly true that geologists define their species more carefully than most taxonomists.

The use of quantitative avoids many semantic arguments. I am a great believer in observations, but these observations should be reproducible.

VOICE: I understand that some paleontologists have named some species stratigraphically. Would you care to comment on this?

GIBSON: I personally agree in most things that time portrays the same thing we find in horizontal points. I think that if we can define sub-species here we will find many times that these may be not as simple patterns, but back through time it would be roughly the same way. Species, in paleontology, is a potentially interbreeding thing. It must be thought of in this way because these animals are no longer with us. I think that we can still find the same type of separation present in paleontology that are represented by subspecies in biology.

MARINE ZOOGEOGRAPHY[1]

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For the systematist biogeography is the first step in the systematic synthesis beyond the recognition and cataloging of species. It is also the essential step in the process towards evolutionary synthesis. Without a clear understanding of the occurrence and abundance of species in various parts of the world it is not possible to understand the evolution of species. Of course we need information from other aspects of the process also, but the biogeographic synthesis is the first necessary step.

In the sea--or in considering marine material--we are confronted with certain circumstances that have not always been adequately considered by biogeographers. In the first place probably the majority of species in most groups are known from very small numbers of individuals. In many instances, from single specimens. Such single specimen records are of little or no value in biogeography. Contrasted with this on the other hand are the vast populations of some marine organisms--such animals as the pteropods and the copepod Calanus finmarchicus may well be the most abundant species in the world, far outnumbering any terrestrial populations. A significant initial approach has been made towards analysis of such populations by Fager and McGowan (1963). The third aspect is the biogeography of benthic assemblages. An attempt at a world wide synthesis of communities was made by Thorson in 1957. However, ecologists have yet to agree about the limits and definitions of benthic communities and the concepts on which Thorson based his "parallel community" idea have not been critically re-examined in the past ten years. On the whole the biogeographic synthesis still depends, as it did a hundred years ago, on the subjective appraisal and judgement of systematists who happen to be interested in problems of distribution. The principal criterion used is the percentage of genera or species found within a certain area, usually defined by temperature limits. The classic definition has been that a region may be recognized as distinct if fifty percent of the species occurring in it are peculiar to it.

Any biogeographic synthesis must be based on the judgement of systematists, and there are two axioms or postulates, diametrically opposite, to be considered.

The first of these is that animals that look alike to the systematist are indeed the same species. Identical animals are therefore the same species, no matter where they occur and no matter how difficult or embarassing it may be to explain their distribution. Failure to consider this possibility carefully may produce skewed results. However, we have come to realise that where there are large populations of a widely distributed species, there may be physiological differences in rates of metabolism or reproductive cycles. The latter may of course prevent interbreeding of separated populations under laboratory conditions. In time this may require definitions of populations according to physiological

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[1]Note: This is a modified transcription due to tape recorder failure.

reactions somewhat after the manner that a bacteriologist recognizes species. This matter will not be considered further here.

The second principle is that animals that do not appear to be morphologically identical may actually be the same species. We are not referring to sexual dimorphism or abnormalities, although there are examples known to most of us of two sexes being described as separate species and abnormalities masquerading under another name.

These two ideas may seem obvious and elementary, but marine zoology in particular is full of invalid species proposed by people who did not believe that a similar animal in a distant part of the world was possibly the same species as one known closer to home. However, one must also be on the alert for the careless systematist who identifies similar appearing material as the same species. We hope this sort of thing is fading from the scene. Nevertheless much of the data of marine zoogeography consists of descriptions of inadequately defined species, many of them based on a single specimen. Some of these have never been found again.

Since my own frame of reference is the Pycnogonida, a group of exclusive marine arthropods, I will discuss some of the problems of biogeography as elucidated by these animals. Most of the 600 odd species known in this group are based on single, or at best a few, specimens. They give us some idea of generic or family distributions. More often than not the type specimens are stored in museums remote for the site of collection. In one entire genus, Colossendeis, we have no record of reproductive condition although we are able to recognize sex. These are the largest of the pycnogonids, common in the deep oceans and most abundant in Antarctic seas. Some of these are common, and there are several records of pycnogonids having been caught in very large number. Usually these are of species of Nymphon, the largest genus of Pycngonida with more than a hundred species. A thousand or more specimens of a boreal arctic species, were taken in a single dredge haul off Scotland some 90 years ago. Pycnogonids are primarily creatures of the colder oceans although there are tropical species. The tropical and shallow water temperate species are small, and not numerous. Some of these appear to have the so-called Tethyan distribution, ranging from the Mediterranean, warm Atlantic to Hawaii. However records of these small warm water species are too incomplete to justify generalizations.

The best known pycnogonid faunas are those of the Arctic and Antarctic regions. In the Arctic there are several recognizable distribution patterns. There is first the group of widely distributed boreal-arctic species of which Nymphon grossipes is the best example. The high arctic species occur in the arctic mediterranean basin north of Canada and European Siberia; they do not reach Pt Barrow on the American side and barely transgress 180°E on the Siberian side. These high arctic species include Colossendeis proboscidea and Nymphon robustum, which are found in deeper North Atlantic waters. There are surprisingly few pycnogonids that occur throughout the arctic and boreal regions of Europe and America. Nymphon longitarse is one of them, possibly Pseudopallene circularis is another. I find no evidence in the Pycnogonida to substantiate the suggestion by Nesis (1960) that there is a group of species that emigrated through the region of the Bering Straights into European waters during warmer periods of time. Pycnogonum littorale, for example, does not occur at Point Barrow or anywhere in the Bering Sea or northeastern Pacific. A japanese species, formerly considered a possible

variety of this common European littoral species, appears to be distinct. An interesting contrast is presented by the pycnogonids that are possible predators of the Octocoral Gersemia rubiformis. In Greenland waters this may be Boreonymphon rubustum. In Oregon the octocoral is infested by Tanystylum anthomasti, a species originally described from Alcyonium for Hokkaido; Gersemia is abundant at Point Barrow and Tanystylum also occurs there. In any event, Gersemia is much more widely distributed than either of its pycnogonid predators. All of which indicates that even for the Arctic regions we still need more information.

The Antarctic pycnogonid fauna is a startling contrast. There are at least three times as many species confined to the cold austral waters, south of the Antarctic Conergence, as there are to the arctic regions. There is not the gradual change to boreal regions in the Southern hemisphere probably because of the vast open oceanic expanses. The nearest counterpart might be the Magellanic. The suggestion by Soviet workers to term the subantarctic regions "notal" does not attract me. "Notal" means pertaining to the back and hardly seems a good opposite for boreal.

One of the conspicuous aspects of the anarctic pycnognid fauna, noted also for other groups, is the development of giants. Another, peculiar to the pycnogonida, is the development of polymerous forms. These may actually be the same species as octopodous forms; certainly such genera as Pentanymphon and Pentapycnon are not really distinct from Nymphon and Pycnogonum. We do not understand this phenomenon, which also occurs in the American tropics, so we cannot say it is a unique Antarctic phenomenon. Interestingly enough the first truly antarctic animal to be collected by a naturalist was the pycnogonid Decolopoda australis, described by James Eights in 1837. If this genus cannot be separated from Colossendeis it would oblige us to change names for a large, world wide genus, and it seems best to consider this as a convenient form genus and ignore the stuffier nomenclatoral matters implicit in the problem of polymerous pycnogonids.

It is obvious from the completely different facies of the arctic and antarctic pycnogonid faunas that there is little support for the idea of bipolarity in this group. This old idea, that the polar regions are inhabited by relicts separated by gradual warming up of the middle latitudes, was originally espoused by a researcher named Theel, primarily on the basis of work with Gephyrea. The concept of the Gephyrea was in itself an indication of naivete, since this was supposed to indicate affinity between apodoous holothurians and annelids - Gephyrea means "bridge". One of the prime candidates for this hypothesis is Pirapulus, an obscure worm, but more critical examination indicates that there are two species involved. There are no shallow water bipolar pycs, and no strictly bipolar birds although there are far ranging migrants. The northern hemisphere counterparts of the penguins were the auks, now alas extinct.

Of course, as pointed out by one questioner later, there are ecological counterparts, both in polar regions and other areas. This says little more than calling our attention to the circumstance that there will be producers, consumers and reducers wherever we go. Crabs, for example, are absent in the Antarctic seas; their ecological role may be assumed by the large isopod Glyptonotus. In Australia all sorts of ecological counterparts were developed among the marsupials for the carbivores, herbivores, etc. of other continents. This is what Darwin saw among the Galapagos finches, for that matter.

So far I have concerned myself mainly with benthic distributions. There is nothing elsewhere in the world so marked as the break between distributions that coincides with the Antarctic Convergence or "polar front". This great hydrographic feature rings the globe, and certain animals and plants do not occur north of it. The most conspicuous of these is Euphausia superba, the krill. There are many statements in the literature that certain bottom animals are confined to the south of the convergence, but in this case depth is probably the controlling factor, since most of the benthic animals being considered occur in shallow water and the continential shelf of Antarctica is narrow. Incidentally it is nothing particularly new to note that the observed distributions of many antarctic animals correspond to the localities of dredging stations. The more information we get, the more species show up to be distributed entirely around the continent in shallow water, that is, are circumpolar. There may be no real differences in the Antarctic, as contrasted with the apparent regional differences noted for the Arctic.

Latitudinal diversity

The euphausiids, incidentally, are an excellent example of the aspect of latitudinal diversity discussed by Fischer and many others. In low latitudes we find a greater diversity of species and relatively smaller populations of each species, whereas in higher latitudes there are fewer species and larger populations. Below the Antarctic Convergence, for example, there are only two species of Euphausiids, and by the far the greatest populations consist of the single species Eu. superba. Now that the Blue Whale is about done for, many have asked the question: are the Euphausiids a harvestable resource? Unfortunately they are a bit small for economical processing, but both Russians and Japanese are looking into the possibility of harvesting and processing the krill, possibly for human consumption.

The problem of marine provinces has been with us since the days of Edward Forbes, who attempted the first biographical synthesis in the 1840's. Forbes had no statistical criteria; his provinces were "centers of creations"; in later years provinces have been simply major regions in which half of the species are different from anywhere else in the world. There have been a number of attempts to arrive at somewhat more objective definitions, notably on the Pacific coast of north America where conchologists in particular have concerned themselves with this problem. For that matter, much of marine biogeography has been based on studies of mollusks, or has been carried out by specialists in mollusks. Carcinologists have also concerned themselves with these problems. For the most part biogeography has been the concern of specialists in the individual groups, and inevitably their concepts of such things as provinces do not agree. Since Forbes we have had only one major attempt at a synthesis, that of Ekman.

Since the days of Dall and Bartsch there have been proposed various regional, provincial or sub provincial divisions for the Pacific Coast of North America. These have been reviewed in my contribution (1957) in the Treatse on Marine Ecology. The most noteworthy of these was the attempt by Schenck and Keen to define provinces according to the mid-points of ranges of the species. This method gave undue weight to species known from single localities, or to regions where much collecting has been done (i.e., places accessible to shell collectors). The latest attempt to define Pacific Coast molluscan provinces is that of Valentine (1966), who has applied such procedures as coefficients of

similarity of pairs, trellis diagrams, and the like. But his results are not greatly different, because the Pacific Coast is a remarkably uniform reach of seashore for a very long distance, and the divisions recognized are of secondary rank. Perhaps it is time to attempt this with some other group than mollusks although admittedly we lack equivalent information. In any event, Valentine has come up with some nomenclature I find disconcerting, especially the designation of Oregonian for the region from 35°N. to 55°N. Those of us with some experience on the Oregon coast consider Oregon, which is in the middle, to be somewhat anomalous or at least less characteristic of the Pacific coast than northern California or Washington-southern Alaska. This seems to be the ultimate expression of the mid-points of range idea! If we look at his subdivisions of the Oregonian we find that from 35 to 38°N. is the Montereyan (this is as far north as Tomales point, which is the northern limit of Lottia gigantea and possibly the southern limit of some crustacea and echinoderms); the region from 38° to 48° N. is termed Mendocinian. This includes the entire Oregon coast, but Cape Mendicino does not occur in Oregon of course. The large red abalone Halitois rufescens is scarce in Oregon and not found north of Cape Arago; the lined shore crab Pachygrapsus seems to give up somewhere below the 45th parallel, and Littorina planaxis is dubiously present at Cape Arago. The subprovince from 48° N. is termed Columbian. I am not familiar enough with this to comment on it. The problem here, as with many other treatments of provinces, is that it is unreal to treat areas of distribution as collections of independent overlapping ranges. I would like to think of a province as not only a center or region of speciation, but a concentration of ecology, so to speak. The differences may well be in terms of physiological species or different breeding periodicities. Further, the physical factors have not been adequately considered. The Oregon coast, for example, is a series of rocky basalt headlands separated by long reaches of sandy shore that may have some effect on the colonization of the separated rocky headlands.

Biogeographic data is an important element for drawing inferences about evolution, and also for giving us some idea of the posiible relationships of land masses in past epochs. Since the pycnogonids have a poor fossil record, they are of little value in this context. Paleontologists have observed similarities in the fossil record of maringe invertebrates that suggest continuity of seas in times past, or a possibly different arrangement of continent land masses. There are so many similarities in the fossil record on both sides of the Atlantic that the record is considfed to substantiate the idea of continents drifitng apart, perhaps in comparatively recent (Tertiary?) times.

The latest contribution to this sort of thing is that of H. Barraclough Fell in Nature for 17 June 1967. According to Fell there is an exponential decay in the number of species of echinoderms as one moves eastward from the center of maximum speciation in the southern oceans. It is not clearly stated what this center is, but it appears to be New Zealand. This is stated to be an effect of the West Wind Drift. It is also true, according to Fell, for mollusks and penguins. In the equatorial regions Fell finds that the exponential decay has the opposite sign, that is, it falls off to the west. There seem to be neutral areas or nodes at about 30° North and South latitides. This conforms to the curve for the Coriolis parameter, Cos 3 ϕ, and indicates a possible connection "between speciation and the gyral system of a rotating planet."

This relationship may be followed in the following recording without considering the position of past land masses, and from this the position of the equator in the past epochs may be inferred. I would suppose that perhaps the shallow shelf areas which provide most of the fossil record might possibly be arranged in a similar manner with narrower bands at 30° or thereabouts; of course this may also be due to Coriolis effect. Many of us view with some skepticism the idea that the fossil record is adequate to support such refined calcultaions, especially the derivation of the position of the equator back into Devonian times.

Somehow this Coriolis hypothesis reminds me of the reverse situation when a geophysicist took an unpublished flier into biogeography. According to this gentleman there ia a band of size sorted pebbles on the bottom just below the Antarctic Convergence. He suggested that this might be explained on the basis that these stones were crop stones of penguins, disgorged for some reason when the penguins crossed the Convergence. Penguins are carnivorous birds and do not need crop stones, and the most abundant ones stay south of the convergence anyhow.

What Fell really says is that we can demonstrate speciation by latitudinal bands, and because these bands have shifted north and south in time we can infer the location of the equator and from that the position of the poles. It seems to me that paleontologists have been doing this for some time without the benefit of Coriolis, e.g., Durham (1950).

Our main concern remains the understanding of the distribution of species in Recent seas, and especially in gaining a more thorough knowledge of quantitative distribution. The nature and stability of the mass populations of the sea will be of incressing concern to us in the future as we develop a greater dependence on the resources of the seas. The task of the systematist will increase rather than diminish as biogeography becomes more quantitative.

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PLEISTOCENE AND RECENT FAUNA

Clayton E. Ray

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I would like to direct my opening remarks to neontologists. If you are willfully limiting yourself in your systematic studies to a single time plane, the present one, and you are working with a group that has any fossil or sub-fossil record, then what you are doing in relation to systematics has no consequence. The time plane should be a part of the everyday working system for everyone.

I will define a few terms and give a few definitions. Pleistocene and Recent are useful and usable terms in systematic studies because they tend to make it easier for would-be pigeonholers to stake out territory and close their minds to fossil or Recent material depending on their job. I prefer to use the term Quaternary, a unit of geologic time which encompasses both the pleistocene and the Recent. The Quaternary is the latest period. The term subrecent has no meaning at all because it can be taken to mean everything back to the Cryptozoic. The Quaternary was originally applied to the superficial generally unconsolidated deposits strung over the surface of the earth. They usually conceal the older, consolidated rocks. The Pleistocene is defined primarily on a climatic or on a faunal basis. Climatically, the beginning of the Pleistocene is defined by the onset of glaciation. The end of the pleistocene is marked by return to warmer climates.

The faunally defined Pleistocene is defined on the basis of the first major faunal-stratigraphic break below the earliest indication of climatic deterioration. The end is defined by the extinction of large mammals.

VOICE: It might be philosophically unsound to define the Pleistocene on the basis of climatic changes. There are changes in the animals which reflect the climate, and none of the other geologic periods are based on climate, they're based on evolutionary changes. Why not use the same criteria for the Pleistocene?

SPEAKER: There are several problems there. One thing, we do try to use evolution and I think that this is possible. One of the practical problems in using evolution as a basis is that is the Quaternary, we are trying to cut the record much finer than it is cut in preceding geologic time. Evolution doesn't seem to work fast enoggh to do it easily. We may be able to do this with certain animal groups, such as micro-mammals. We also try to use migration. Radiogenic dating is our best hope for putting the two together.

The Quaternary is highly atypical in earth history; glaciation, radical changes in sea level, vast faunal changes, migrations, range changes, and extensive extinction. These are important events. And we have lots of evidence in the Pleistocene. It is near the present and there hasn't been much time for the record to be destroyed. There are so many fossils that it is hard to unravel it.

Systematics has a phylogenetic basis, therefore has an evolutionary basis. Someday, the students of DNA may be able to take an organism and say what steps inevitably had to be gone through to reach that present organism.

Fossils of vertebrates are generally found broken up, and this to me is generally just an annoyance. It shouldn't scare a systematist of living groups away, but it does..

Until very recently, it was always understood in vertebrate paleontology that if you insisted on doing anything with pleistocene fossils you should at least be embarassed about it. In the past this sort of attitude has resulted in very poor work in the Quaternary. The work has been done in the past largely by incompetents.

One of the groups that has been said to benefit almost not at all from Quaternary fossils is the Bird group. There are very few paleo-ornithologists, and now more bird bones are being found. The most important thing in the study of evolution is the origin of species, and how can you pretend to study the origin of the species, in particular, of the species that you are working with, without studying the fossils of the last two or three million years? (We have to make exceptions for groups that are extrememly long lived or short lived.)

I am going to talk about mammalian systematics. It has been said that we construct a phylogeny on the basis of a few bones or hard parts. It seems to me that the systematics of mammals is almost moribund, no one besides mammalogist is interested in what they are doing. I think that both the fossil and the modern populations of mammals need to be studied by the same individuals. It isn't enough to be aware of the literature of the other group.

The very best workers on Quaternary fossils are going to come from the ranks of neontologists.

Our progress is impeded because we are victims of what is a theoretically indefensible housekeeping arrangment.

I would now like to illustrate the relevance of the Quaternary record to the systematics of living groups through a couple of examples, the polar bear and the musk ox. The polar bear is assigned to its own monotypic genus, Thalarctos, and it is the most highly carnivorous of the living bears.

The fossil record for polar bears consists of a half mandible, one right femur, two partial skulls, fragments of a humerus, a scapula, three ribs, and one left upper canine and one partial ulna. That is all. Only the ulna is of full glacial age. The others are late glacial and even post-glacial. And only the two skulls constitute a population sample greater than one. They come from the same beds, and the same spot. The polar bears seem to show a decrease in size, post-glacially, which is a common feature in many mammalian groups. I would go so far as to say that the polar bear origin is a direct result of the Pleistocene glacial advance, and I think that it developed within the last hundred-thousand years of it. We have evidence of a very rapid evolution and a sharp change of direction in the development into the modern polar bear.

Another example I would like to bring up is the Musk Oxen. They are now limited to a single species, Ovibos moschatus which is limited to the North American Tundra. The fossil record of Ovibos and of Musk Oxen in general is quite a rich one in the Quaternary. They ranged from the

British Isles, southern France, across through Asia and throughout much of North America. The living species may have survived in Siberia until very late times. Ovibos seems to be developing a spherical shape as well as it can; short legs, drawing the horn cores in, short muzzle, shorter neck, blockier body. Studies have been done on horn cores of living goats and antelopes, and by countercurrent heat exchange it has been shown that the horn core acts to regulate the temperature of the animal. Heat loss from long horns and long slender legs could be serious to Ovibos. It has been suggested that Ovibos' projecting orbits may be a guide to the depth of the pile of the wool hair.

Another thing I would like to bring out is the matter of communities. What does it mean to the survivors when approximately half of a species in a community die out? One of the things we were discussing were parasites. Were there host-specific parasites on the mastodon, for whom it meant the end of the road when the mastodons became extinct. I think that there were. What would it mean in Africa today if all of the Proboscidians and most all of the large herbivores were wiped out? That happened in North America in late Pleistocene time.

DISCUSSANT

Thomas R. Waller

United States National Museum

As a result of Ray's presentation, neontologists are either going to begin taking a closer look at the fossil record or they are all going to begin switching to groups with no fossil record.

There are three points I would like to bring out, three ways neontologists and paleobiologists might be brought closer together. One is that the paleontololologists have to provide a better dating framework for neontologists, particularly in the Pleistocene. There has always been a lot of confusion about this and especially about the definition of the Pleistocene. There is also a tremendous lack of agreement between the vertebrate and invertebrate paleontologists on the final significance of different kinds of fossil remains. The thing that has come along that is going to help everyone is radiometric dating within the latter part of the Cenozoic.

The other problem is the old conflict between what we must call paleontological and populational systematics. It is significant that people working in what has been called numerical taxonomy are calling it a revolution in systematics. But the people working in populational systematics are calling their operation in systematics a revolution. We simply have two overlapping revolutions. I think that as populational systematics becomes more ingrained in terms of zoology and paleobiology, people are going to be looking at more characters by means of numerical techniques. Computers have been used very effectively in populational systematics by looking at characters in new ways and looking at ontogenies.

On the whole, I think there has been a reluctance on the part of paleontologists to look at the soft parts of organisms and to use them to get ideas about the adaptive significance and changes that they see in the hard parts. And also, there has been a reluctance among the zoologists to try to find out what the variation is in the preservable parts of the organism.

The third point has to do with a consideration of the geological physical processes in reaching systematic conclusions based on the study of living organisms....

ECOLOGICAL EFFECTS AND SYSTEMATICS

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The Relation of Ecology to Systematics

Williams(1966) proposed teleonomy-a field of biology that seeks to answer the question of, "What is the function of a structure?" Williams further suggests that systematic studies are not likely to lead to important advances in understanding evolutionary adaptation. I must agree with Williams, but wish to point out that teleonomy is a branch of systematics. Efforts to answer the question above will frequently be by comparison of taxa that possess or lack a certain structure and any comparative study contributes to systematics, so I would disagree with Williams at that point.

Systematics should be study of evolution at all levels with the comparative approach as its major working format. The taxa that are distinct today regardless of their categorical rank were, at their inception, part of a single species. All of the selective forces responsible for their evolution and speciation were ecological forces. By this I mean they were environmental forces broadly defined. This would include all aspects of the environment from the genic to the demographic to the physical and biotic. It is also true that the higher we go in the hierarchical arrangement of taxa the more difficult it becomes to understand the origins of certain traits. For this reason I am going to concentrate in this section on evolution at the species level and below.

I will take the point of view that the origin of some characters and the reasons for their perpetuation can be understood by intensive ecological study of different populations of the same species or of different closely related species under allopatric and sympatric circumstances.

In my abstract for this conference I outlined various stages in the usual process of divergence and speciation and explained how ecological factors are involved at each level. I am going to emphasize in my discussion not the importance of ecological data per se in constructing classifications or inferring relationships, but for understanding the origin and function of traits, because ecological data per se are probably not especially useful. Nothing of evolutionary importance occurs above the level of the species, despite some arguments to the contrary.

I would like to begin by discussing some of my own work with the lizard Uta stansburiana.

Evolution at the population level in Uta stansburiana

Uta stansburiana is a highly variable small species of the large lizard family Iguanidae. It has undergone most of its evolution recently on islands in the Gulf of California, a story to which I shall return later in this discussion. On the North American mainland there is a single species with four recognizable geographic races.

Slide 1-

Detailed taxonomic study of tese by Royce Ballinger and I shows that

[illegible] EFFECT ON [illegible]

[illegible] on [illegible]

[illegible] of [illegible]

[illegible] discussed [illegible] [illegible] [illegible]

the southeastern and southwestern race are very closely related with a coefficient of difference higher than 90% in only a single character (of 28). Both differ from the northern race in a number or respects, but the southeastern differs more from the northern than does the southwestern because the latter two are intergrading, while the southeastern race is completely allopatric to both of them.

The southeastern and northern races have been subjected to intensive study in the field (5 generations in the southeast and 2 in the north). In these studies we have carried out a number of field and lan experiments, but the bulk of the data comes from nearly 4,000 marked lizards. We attempted each generation to mark all adults and the young that they produced on 2-acre study areas and to follow these animals until they died or disappeared to measure such things as growth, population turnover, life expectancy and movements. In addition, long term observation was made of selected individuals to learn some details of their behavior.

This study proved of value in the interpretation of some of the marked morphological and behavioral differences between the two populations and in explaining the origin of some of these observed differences.

The degree and function of aggressive behavior

Both sexes in Texas are highly aggressive. The aggression almost certainly has a genetic basis and the high degree of aggression could have arisen and become characteristic of these lizards only if the aggressive individuals left more genes in the population than the non-aggressive ones. Thus, regardless of other results of aggression such as dispersion in relation to resources, it must result in a higher fitness. This, however, is more a theoretical probability than a demonstrated fact for natural populations. However, in my studies I have been able to find evidence of the fitness values of aggression. This has been demonstrated as follows:

1. Show territory dispersion size--I assume that the size of the territory is probably a useful measure of the degree of aggressiveness of the individual.

2. How fitness is measured

3. Correlation of fitness with territory size

4. Increasing strength of this correlation as density increases

Williams(1966) has argued that such differences that I have noted may be understandable only by reference to the demography of the population. Here, and in subsequent sections, you will appreciate my debt to Williams for his lucid treatment of this and related subjects.

The demographic facts with regard to the Texas utas are that Texas lizards experience at least a 90% annual turnover of the adults. Rarely does an animal live to participate in two breeding seasons. They have, then, essentially one opportunity to reproduce. Therefore, maximum effort must be expended in one season and any feature that enhances their reproductive performance such as aggressive behavior will be favored. Indeed, it is favored to the extent that social hierarchies maintained by submissiveness of some individuals are not ordinarily established.

The effort expended by a Texas female in reproducing may be appreciated by consideration of the fact that in an average breeding season of about 4 months, a female may lay 4 or more clutches of eggs representing a

synthesis of yolk material exceeding her own body weight.

Now, let me turn to the situation among the Colorado lizards. My preliminary impressions of them were that they showed no aggression or social interactions at all. These impressions were based upon 3 observations, all in marked contrast to what was observed in Texas:

1. Several home ranges (territories) when plotted were nearly congruent.

2. No social antagonism was observed in the field.

3. Colorado lizards in the laboratory showed no social interactions.

I later tested the aggressiveness of these animals in the field. The residents did behave aggressively but only weakly compared to Texas. Submission often resulted or only short movements away by the non-residents. Both types of behavior were sufficient to deter further challenge by the resident. Furthermore, among lizards with overlapping territories there was definite observational evidence of social hierarchies of one or more dominant lizards that performed most of the courtships and aggressive posturings and a number of other lizards (and younger ones) that were submissive to dominants whenever they appeared.

Sexual dimorphism

Recall that the degree of sexual dimorphism is far greater in the Texas than in the Colorado lizards. This could be attributable to a number of factors:

1. background matching by the saxicolous Colorado lizards

2. evolutionary history

3. demography--I lean toward this one because it accounts nicely for the great variability in the expression of sexual dimorphism in this lizards.

It has already been pointed out that Texas lizards over several generations have shown essentially no overlap of age classes during the breeding season. However, a third or more of the Colorado adults survive to a second season and half that proportion survives for three. Consequently, they have more than one chance to reproduce. If a female, for example, is relatively non-aggressive she may be relatively unsuccessful at breeding during her first season, but may live to outreproduce the dominant aggressive female at least in some years--by virtue of her less conspicuous behavior, she may be less subject to predation. The individual lizard, unlike the situation in Texas, is required to expend less effort at reproducing because her reproductive life expectancy is longer. Thus the genes for aggressiveness in the demographic environment of Colorado lack the selective advantage that they enjoy in Texas.

The greater sexual dimorphism in Texas can then be explained somewhat as follows. A Texas male that is highly aggressive will benefit by also being bright and showy. The only way in which a male can increase his fitness is by breeding with as many females as possible. The showy colors may aid in attracting females and in intimidating rival males. In the Colorado lizards such coloration and display in a male would be

less advantageous because it would not necessarily disenfranchise other males and might limit its own survival.

The importance of the demographic environment as a potent factor in selection is perhaps even more clearly appreciated by considering some birds such as large raptors in which the age of immaturity is lengthened. One would ordinarily expect selection to shorten the pre-reproductive age. Another fact about these birds is their very small clutch sizes. However, the low reproductive rates could be means of insuring the production of large, strong highly competitive young. The delayed maturity could come about by selection against early reproducers if, by their inexperience and inability to defend large territories, they are able to rear less competitive offspring than older birds with larger territories and greater food gathering ability (Amadon, 1964).

The evolution of size differences in Texas and Colorado lizards

In Texas, utas hatch in mid-summer and reach a mature size in late fall or early winter. That these animals are also physiologically mature has been demonstrated by laboratory experiments. However, this physiological maturity is not reached until a snout-vent length of 41-42 mm, the minimum size at sexual maturity.

Colorado lizards despite their much longer life expectancy are smaller. Paradoxical as it may seem, I would like to discuss a body of evidence that suggests that the evolution of smaller body size in Colorado has resulted in increased fitness.

I have stated earlier in discussing the distribution of utas on the mainland that the Colorado lizards have been secondarily limited to norther areas. Similarly there is reason to think that the Texas lizards have always been southerly in occurrence.

The Colorado lizards hatch a month later than in Texas and have a shorter growing season. They mature at a smaller size (36-37 mm in snout-vent), but even so nearly one-half of the females are still immature at the onset of the spring breeding season. Suppose that they had to reach the same size as the Texas lizards in order to become physiologically mature; obviously a still smaller fraction would be able to reproduce during the first breeding season. Consequently, in this population a lizard capable of breeding at a smaller size would have a reproductive and selective advantage. However, selection for a small size at maturity would also have the effect (unless egg size were decreased--it isn't) of decreasing the number of eggs the female could produce. In almost all lizards studied to date there is a positive correlation between increasing body size and increasing clutch size.

Some additional behavioral differences between Texas and Colorado lizards.

Species discrimination

The Colorado lizards are exposed to other species of iguanid lizards that are of a sufficiently similar size, shape and pattern to be potentially confusing to a uta. The Texas lizards are not coexistent with any potentially confusing species. Consequently, one can predict that a Texas male, for example, might be less capable of discriminating against a female of another kind that would a Texas lizard. This hypothesis has been tested by Gary Ferguson and Charles McKinney this summer.

Texas and Colorado males were given simutaneously females of their own populations and those of the other population. As predicted, the Texas males chose at random (6 right, 6 wrong) while Colorado males were significantly more discriminating (12 correct and 2 wrong). It is of passing interest that Texas lizards in the lab did show discrimination ability.

Differences in assertion behavior, courtship and copulation

Most iguanid lizards show push up bobbing behavior, the function of which is not understood. However, it has been said that such behavior is species-specific and there is some experimental evidence (Hunsaker). To indicate that female lizards are attracted to a bob like that of the male with which they are ordinarily associated. If so, such bobs could serve as at least a partial isolating mechanism.

The bobs of Texas and Colorado lizards are similar, but not identical. The Colorado lizards have 5-component bobs, while the Texas lizards have 4.

More striking differences exist in courtship and copulation. The Texas male generally circles the female several times during his courtship approach. He does relatively little nipping and licking before attempting to grasp the female to attempt copulation. The Colorado male does not circle, but approaches the female directly and spends some time licking and nipping at her before attempting copulation. During copuiation the Texas male performs less than a half-dozen pelvic thrusts during copulation and remains in copulo less than 30 seconds. The Colorado male thrusts a dozen or more times and remains in copulo more than a minute.

Significance of these results

There is general aggreement in the literature, although such literature is not voluminous, that what are called isolating mechanisms are mechanisms for increasing the efficiency of mating within a population. As such they may develop in different allopatric populations of the same species, fortuitously as a result of the differing ecologies of the two populations.

Size, aggressiveness and efficiency of mate discrimination might be influenced pleiotropically by the same complex of genes that determine other behavioral or structural differences. These differences might prevent or make ineffectual interbreeding between the southeastern and northern races of uta should they become sympatric.

Some information from other animals

Crook in a series of papers on the African and Asian weaver birds has provided some nice examples of the power of ecology in explaining some fundamental differences between various species of these birds.

Specifically, the mating systems of monogamy versus polygamy seem to be related to the available food supply in the types of environments occupied by these species. For example, if food supply is predictable then a species will expand to the point at which food becomes limiting and regulating. Under such conditions there will be considerable intra-specific competition for food. As a result, the fitness of both male and female may be improved if they cooperate in rearing the young.

On the other hand if food becomes available in large quantities rather suddenly during the breeding season, then intraspecific competition for food will be lessened and the best strategy for a male may be to mate with as many females as possible since the females will be able to find sufficient food to rear the young without his help. In other words, polygamy may be favored. Because it is unlikely that most birds can gauge the food supply directly at the onset of the breeding season and behave accordingly it follows that such differences in mating behavior are probably genetic.

Orians has likewise invoked ecological opportunity in his studies of social behavior in the blackbirds and, by implication, other species.

Orians notes, for example, that if 2 species formerly allopatric became sympatric and were already ecologically compatible and hence non-competing, then selection should eliminate tendencies toward interspecific aggressiveness. However, if the two species were incompatible then aggressiveness, already present because of intraspecific factors, would be maintained. The latter is apparently the sace of the tricolor and red-winged blackbird studies by Orians in California.

Reproduction in the great Tit (Lack, 1965)

As you are aware Lack has long been one of the chief proponents of the idea that birth rates represent the maximum possible under prevailing conditions and have nothing to do with juvenile mortality rates.

Some data seem contradictory to his point of view. For example, the great Tit laying in coniferous forest in Britain lays 9 eggs on the average which is the number from which the greatest number of nestlings survive in the oak forests of Britain where there is a rich source of caterpillar food for these birds. However, in the clutches in coniferous forest many hatchlings starve, suggesting that the clutch size is not adapted to the number of young that the parents can successfully rear. This situation is made perfectly understandable only by reference to the evolutionary history of the Tit. The oak forests were evidently its original habitat in which selection has adjusted the clutch size to a mean of nine eggs. The conifers are a less productive habitat, but they are not geographically separated from the oaks so that the genes for 9 egg clutches are still characteristic of birds living in pines. Presumably, in time selection will adjust the clutch sizes of such birds to the environment.

This example serves to illustrate one of Orian's (1962) major points that while it is possible to look at the ecology of a population without considering its evolutionary history, such a point of view is likely to be misleading.

Additional examples from lizards

Before concluding this section on evolutionary mechanisms at the population level I would like to give one or two cautionary examples of how considering ecology too strongly may allow erroneous conclusions to creep into systematic studies.

Soule made a careful if incomplete study of the phenetics of the island lizards of the genus Uta in the Gulf of California where they have undergone most of their evolutionary divergence. He concluded that the evolution in the Gulf could be explained by the difference in the ecologies of the various islands such as island size, distance from the

mainland, etc. and the probable influence of these factors on the genetics of the different island populations. Let me take one character as an example---the size of the dorsal granular scales characteristic of the entire genus.

The scale size is quite variable in the genus. There are some species or races with high numbers of small scales and others with a smaller number of larger scales. Because scale number and therefore scale surface area might be important in thermoregulation, Soule concluded that scale number was a highly ecotypic character strongly influenced by local selection on islands with differing thermal environments. There is no doubt that scale size is a labile characteristic and according to Soule's hypothesis we would conclude that a group of species with high scale numbers were related phenetically, but not phylogenetically.

However, both scale patterns--small and large occur on the mainland. In fact in one area of Sonora they occur sympatrically in Uta s. elegans and U. s. taylori. The closest relative on the basis of many other characteristics of the small-scaled taylori is U.s. stansburiana in Colorado. This begins to look as though evolutionary history and relationships are involved. This interpretation receives support from tests of mating behavior.

Convergence seems less likely as an explanation considering the fact that we must assume many multiple occurrences of the same trait. It seems more parsimonious to assume that the islands were invaded and reinvaded at different times in the past by stocks that were differentiating on the mainland. As pointed out previously at least 2 such stocks are still extant on the U.S. mainland.

Sympatric speciation

Another subject worthy of much more investigation at the level below the species is sympatric speciation. Of course various models (see Maynard-Smith for example) have been proposed for the operation of this phenomenon, but....

Certainly everyone would agree that the probability of sympatric speciation is less than for allopatric. This is partly due to theoretical consideration, but also to the demonstrated fact that there are many more examples of species formation from beginning to end (geog. variation to allopatry, etc.) that are readily interpretable by allopatric models.

It is also clear from the work of many such as Sheppard on mimicry that disruptive selection is a powerful force. The research of Thoday and his coworkers and Streams and Pimentel on laboratory population of Drosophila make it clear that strong disruptive selection can overcome rather massive gene flow and allow divergence of two parts of an essentially random breeding population without isolation as predicted originally by Mathes. Therefore, the stage for sympatric speciation might be set in any polymorphic population in which there was strong selection for both types. Gene flow might, in such cases, become indirectly restricted if the two types had different habits:

food
habitat --- imprinting to these might allow isolation during breeding season.

I'm not, however, going to talk about possibilities, however interesting. I am instead going to detail a case of almost certain sympatric speciation and one that is particularly relevant to a discussion of the role of ecology in systematics. I refer to the work of Alexander on eastern U.S. crickets.

The ranges of Gryllus pennsylvanicus and G. veletis are essentially congruous suggesting no past allopatry. The songs, among the most important isolating mechanisms in these crickets, are nearly identical. The two species have differing life histories. G. pennsylvanicus overwinters as an egg and develops into mature adults in the summer or fall of the succeeding year. In the second species overwintering nymphys mature sexually in the spring. The fact that such different life histories did not arise allopatrically is indicated by the absence of pairs of closely related allopatric species of crickets that possess different life histories.

Furthermore, there are no species of orthoptera in which adults from overwintering eggs survive long enough to overlap during the breeding season with adults from overwintering nymphs. No reason, therefore, exists for suggesting that the ancestral population to G. veletis and pennsylvanicus was an exception to this rule.

The hypothesis of Alexander

1. In part of the range of the ancestral species all stages except the the resistant ones (all crickets are resistant only in the egg or nymph stage) were killed during successive winters.

2. Such elimination produced egg and nymph overwintering populations. This, then, inhibited gene flow within the population between adults emerging from the 2 different resistant stages.

3. Even if the adults did occasionally overlap seasonally (rare because of their short life expectancy) it would be during mid-season and the eggs produced would not be in a resistant stage by the onset of winter, so selection would reinforce obligate diapause in the egg or nymph stage and further restrict interbreeding between the two types.

4. Finally, there is a present species Gryllus firmus with life history characteristics requisite to the ancestral type. In the southern part of its range it breeds more or less continuously but in the northern part of the range it becomes an egg overwinter with 1 brood per year. However, a few non-diapausing late juveniles in the northern part of the range of firmus do manage to overwinter in that stage and mature in May and June. Should a northern segment of G. firmus become isolated from populations in the south in an area where the species now overwinters in the above 2 stages, then the scene would be set for speciation of this northern stock while still sympatric.

This is an obvious case in which the course of evolution was fortuitously determined by the environment in which the population ancestral to G. veletis and pennsylvanicus lived. The example suggests that attention to environment in relation to the distribution and habits of a species may reveal further instances, but I will leave further details and speculations to Dr. Alexander.

Isolating mechanisms, reinforcement and character displacement

This ia a very rich area to look for examples of ecology in relation to systematics as the following speculations should make clear. If 2 allopatric populations have become sufficiently divergent so that, following establishment of secondary contact, there is some incompatibility between the genomes when they are recombined in the hybrids, then reinforcement of premating isolating mechanisms is possible. However, such reinforcement is not likely to occur unless the degree of sympatry is rather great or selection against hybrids is exceedingly severe. This is because of gene flow into the narrow region of sympatry from the much broader area of allopatry.

Other questions that might be asked is how often are strong pre-and post-mating isolating mechanisms developed in allopatry during the course of raciation and how often are premating mechanisms reinforced after contact is established.

The literature on this problem is not really so great as one might expect. I have made recently a fairly detailed review of the isolating mechanisms of anuran amphibians, so I will use these animals as the examples in the following discussion. Details may be found in the papers in the bibliography provided to you.

The anuran call has been shown to be a mate attractant and the ability of females to discriminate between similar calls has been demonstrated, although in only very few instances. Mate discrimination in the field has not been demonstrated, but the circumstantial evidence of few mismatings in cases where several species breed in the same pond is fairly satisfying.

The call can be quantified into components and such sonogram records suggest that the pulse repetition rate is the most important component for species discrimination. Hybridization experiments between many species provide data on the extent of postmating incompatibility.

	Allopatric species	Sympatric species
Weak call differentiation	62%	0%
Moderate to strong call differentiation	38%	100%
Postmating mechanisms	17% of those checked	10% of those checked
Actual discrimination tested	19%	27%

** these data provide little support for Mecham's assertion that postmating mechanisms are delayed in sympatric species because of hybridization and backcrossing.

These data do suggest that postmating mechanisms arise as by-products of ordinary geographic variation and are reinforced in many instances after sympatry. Of course the possibility remains that many of the

allopatric comparisons are really between populations that have not reached the speciation stage isasmuch as the same type of direct test of sympatry cannot be used.

Some comments on reinforcement

I have the feeling that many people have taken reinforcement for granted. However, among Anura there are only 5 examples, so I will mention all of these briefly.

1. Microhyla carolinensis and M. olivacea

These have calls that differ the most in the narrow zone of overlap. However, the critical component of pulse repetition rate is not different. Furthermore, at least 1 of the 2 differing call components is correlated with body size which varies geographically in opposite directions in the 2 species so that size differences are greatest where they overlap.

2. Bufo compactilis, cognatus and speciosus

B. compactilis and cognatus are allopatric, but closely related and do not differ in call. B. speciosus and cognatus are "equally" closely related, sympatric and differ strongly in call. Bogert suggests that the difference in calls has arisen as a result of sympatry. However, absence of study of call variability allows alternative suggestion that calls were different prior to establishment of smypatry.

3. Acris gryllus and A. crepitans

Until recent work by E. Nevo this looked like a good example of reinforcement because in one area in Mississippi where the two species overlap, the calls differ in every component despite essential identity of calls of crepitans west and gryllus east of the zone of overlap. However, Nevo by detailed geographic study has shown correlation of the call characteristics with clines in body size and finds no evidence for reinforcement. In fact within one of the species size differences in different parts of the range have altered call to point where females from another part of the range cannot even hear the frequency called by the male.

4. Pseudacris nigrita group

Females of triseriata from Oklahoma can discriminate against call of male feriarum with which it is sympatric, but cannot discriminate between its own male and that of nigrita with which it is allopatirc.

Criticism: this may mean nothing--may be simply fortuitous--explain

5. Hyla ewingi and H. verrauxi in Australia. This is by far the most thorough and certainly the most convincing study of reinforcement yet presented.

Few differences exist between the allopatric populations of ewingi, even between insular and mainland ones. Furthermore, the differences between those populations of ewingi and those of verrauxi that are allopatric to one another are minor.

In the area of sympatry there is virtually no overlap in the call

components; verrauxi is more modified than ewingi. The pops. of verrauxi that are sympatric with ewingi differ strikingly from other verrauxi populations outside the zone of sympatry.

This is the only really convincing case among the anura and I suspect the ratio may be about the same for other groups.

Character displacement

The same phenomenon that produces reinforcement may also produce character displacement. One of the most striking examples of this phenomenon are the hundreds of species, many sympatric, of the genus Drosophila in the Hawaiian islands. Apparently most of the speciation has been from one or a very few founding stocks, so all of these species are closely related. The major differences appear to be in structures important in mating--characters which we would expect to be easily displaced since they may serve as premating isolating mechanisms. I would suggest that practically all cases of character displacement may involve structures important some how in mating, e.g. in mate recognition. Character displacement may also, particularly in birds, involve trophic structures. The Geospizine finches of the Galapagos islands are a classic example, but even in this case the size and shape of the bill may be of importance in mate recognition.

I am not going to talk about this matter in detail. It is obvious that close attention to ecology is necessary in proper interpretation of this phenomenon. It can be demonstrated only when the differences in some structure or characteristic are greater in the zone of overlap of two species rather than outside of it and only when reserve patterns of variation do not occur. Consequently, the demonstration of coexistence in the field is necessary and collections should be made systematically within and outside this zone of coexistence. The recent study of Schoener is the type that is not likely to be of much help. He simply looked at sympatric congeneric species of birds with museum material without knowledge of the presence or absence of actual coexistence at the localities where the animals were collected. If Lack is correct in his feeling that birds are limited primarily by available food outside the breeding season, then character displacement in bill size may be likely because it may alter the niche relationship and reduce competition between species.

I would like to conclude this section by pointing out that there are weaknesses in most studies of character displacement just as there are in those on reinforcement. More careful and detailed studies are needed with an ecological orientation.

The role of ecological opportunity in adaptation

I think most biologists now agree that the entrance of a species into a new adaptize zone may open the way for the evolution of a group that we would recognize as a higher taxon. Thus, the origin of these higher categories is just a special and rarer case of ordinary natural selection. I think most of us can think of classic examples of the radiation of a group that was evidently made possible by entering a new adaptive zone or being able to exploit a rich environment in the absence of competitors. Examples that come to mind are the geospizine finches, the drepaniids of Hawaii, the mammals at the beginning of the Cenozoic, and the fishes of Lake Lanao and other lakes.

We may perhaps see the origins of some of these adaptations at the population level as I have already indicated in utas. At the level of different species there are also some suggestive studies, one or two of which I will discuss as possible examples.

Mating systems in birds

Crook has made several studies of the breeding biology of weaver birds of Africa and Asia. Some of these species are polygamous and some monogamous, but these fundamental differences in breeding structure are not taxonomically predictable, but seem to Crook explicable only in terms of the populat on ecology of the various species.

His hypothesis is as follows. If food supplies in the environment are predictable (e.g. in the tropics) then the birds will expand in numbers until food becomes limiting and regulating.

Ecological opportunity in the evolution of utas

I would like now to give you more details on the ecological data accumulated on lizards of the genus Uta that seem important from the systematic and evolutionary point of view.

As already mentioned the genus is a small one of perhaps a half dozen species (there are many more names than this in the literature, however). It has had a seemingly conservative history on the North American mainland where there is a single polytypic species. However, there are several recognizable forms.

Slides of mainland utas

I would like now to show you some of the island habitats and island lizards and talk a little about ecological opportunity, including its limitations, for explaining the characteristics of the island utas.

Slides of some of the islands

The islands themselves have had diverse histories. Some are simply results of sea level changes that cut portions of the mainland off as isolates. Evolution of lizards on these has been obviously influenced by reconnection to the mainland or by gene flow across a narrow water barrier. Some islands are recent volcanics (Tortuga), some are quite old fault blocks off the mainland from which they are separated by deep channels. Some are very large, others very small, some richly vegetated, some almost unvegetated. All such characteristics have obviously played a part in shaping the populations of lizards that inhabit them.

There has obviously been opportunity for genetic drift, founder principle, cobvergence, etc., to operate, but I think I can show that really only multiple invasion and isolation are really necessary to explain what we see--plus ecological opportunity.

Things to discuss

1. evidence of at least 2 stocks--morphology and behavior

2. How the deep water and isolated islands of Tortuga and San Pedro Martir prove the rule. Old and isolated Martir has a distinctive species

of the primitive stock. So should Tortuga, but when it was formed and became suitable for colonization, there was no invasive primitive stock around.

3. the evidence for and against convergence--Soule

4. The evidence against genetic drift and convergence of Savage--Santa Catalina and San Pedro Nolaso.

5. the occupation of unusual niches and the evolution of unusual size (genetic or ecotypic--discuss lab. data on survival of U. palmeri)

Here very close to home is an opportunity to study in several groups of lizards the evolution of a group with reference to their present and past environments, their associates on the islands etc. Here is a chance to find out, for example, how the presence of Streptosaurus has influenced the evolution of the utas sympatric with it.

Practically every evolutionary problem that exists is present in the genus Uta and is in need of much further investigation--an opportunity of which I hope to take advantage on the next few years.

I'm afraid I've given a presentation that was a bit too rambling and diffuse, but I hope I've convinced you of at least one fact. Though systematics and ecology are justifiable entities in their own right, they are mutually enriching.

To a systematist interested in evolutionary mechanisms, it is of great value to look for the actual selective advantage of certain characters. There is a critical need for this kind of field data that bridges the gap between taxonomy and population genetics and between both of these and evolution. There are few data from nature on breeding structure, mating behavior, social behavior and the influence of these on the characteristics of organisms and on the potential rates of evolution of the demes involved. The systematits should be involved more in such studies. Similarly, the ecologist should be aware that there are vast variations between populations in their ecological characteristics, even within the same species. They must be aware that a long evolutionary history may be behind some of the traits he observes, e.g. the scale sizes of the utas as I have discussed in this report.

I would urge that the comparative approach which is practically the unique property of systematists will be of tremendous value in all of the biological disciplines which will and have gained by such comparative studies and will contribute greatly to systematics in the process.

I see systematics as a field with a bright future in which the triumphs to come will exceed those of the past and I think many of them will come through detailed studies of natural populations.

VOICE: What sort of scale is used in your range maps?

SPEAKER: It is a two acre area, 300 x 300', 9000 sq. ft. This area in the map is 3500' sq.

VOICE: Why are the territories so dispersed?

SPEAKER: The open spaces correspond largely to open spaces on the ground itself. These animals are extremely reluctant to cross open areas. This is an area of mesquite and sand sage with a lot of bare ground, windblown sand, so their movements can be restricted to these vegitated areas. Also, if you are trying to measure the actual perifery of the home range, the probability of getting the animal at the perifery as opposed to the center is remote.

VOICE: Do these animals defend the whole home range?

SPEAKER: They defend even the outer boundaries, but they do show stronger agression around certain sites.

VOICE: Is there any correlation between agressiveness and apparent size of these home ranges?

SPEAKER: A female that gets into an unfavorable part of the territory, will have to patrol a larger area to get enough food, and therefore will be less agressive over the very large area. No one else would really fight her for the unfavorable territory, while a female with a better territory, a smaller, one, would have to fight very agressively to defend it.

VOICE: Could one also argue that agression takes a fair amount of energy from the animal and there might be more favorable ways in which the animal uses his energy?

SPEAKER: This question cannot be answered satisfactorily. It might be that polar bears could get along better if they were a different color too. But the fact is that they are stuck with being white. These lizards may be able to do something better if they were less agressive, but the fact is that selection favors agression.

VOICE: In measuring the fitness of the females, you say you were able to follow the young all the way through the population. Have you followed it through enough to make any correlation between successive females in the fertile generation and successive females in the f4 f5 generation?

SPEAKER: No, I wish I could. Maybe by proper stastical treatment. There are a lot of variables envolved.

DISCUSSANT

Martin A. Buzas
U.S. National Museum

This has been a very interesting kind of discussion this morning for me. I come into this field from geology and paleontology. I am now a marine ecologist. Maring people actually are not usually considered ecologists, rather marine biologists. And yet if evolution and adaptation and the general theory of life are to be developed we must bring maring and terrestrial people together. And we must also try to bring them fossils, because they are working in the recent and always say they are going to have to bring time in to really see what the historical influence did. If we are ever going to get time into the picture, then we are going to have to work with organisms with a good record in time. And if population characteristics are truly very important, then we are going to have to work with organisms where you can have some chance and measuring characteristics. These are mostly marine organisms with hard parts. And I think that it has been almost universal that we have neglected to do this in the maring science. Finally, once you look at what is relative abundance really like, then the question of how can we compare these things comes up. And this would bring in the question of what is bio-facies, what is the relationship of a bio-facies to a community, and how can these things be compared. And it is very easy to talk about these things in a qualatative way, but when you are out in the field it is not so easy.

The next question to ask is one of scale, and how large a scale do you need before this thing breaks down. One doesn't agree with the traditional allopartic-sympartic breakdown working in the marine environment. Because if you define some set of organisms like this, and another set over here, clearly these two sets are not overlapping. In the long run, a different kind of designation like allopatric and sympatric won't be enough. We need something better to tell when two things are separate and when two things are the same.

VOICE: This is the first time during these sessions that anyone has come to grips with the problem of speciation in the sea. But you didn't mention larvae???

SPEAKER: That complicates matters immensely. Although the species may have a rather large range, when you go into the field, you find things living in aggregated masses. And how exchange between these aggregated masses began. But I think that the whole question of trying to measure population characteristics in the marine realm, and I say that some of them can be measured. And hopefully can be measured in fossils. This is the only way we are ever going to get at bringing any time into it at all, into population characteristics and what this means as far as evolution is concerned.

MORPHOLOGICAL STUDIES IN SYSTEMATICS

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Comparative morphology has several aspects of almost unique significance for systematic studies. It provides the great bulk of evidence for systematic studies of the higher categories (genus and higher). It provides much of the needed evidence and examples for formulating general concepts of systematics, phylogeny and evolution at these higher levels; for example, most of the principles of comparative biology have been formulated on the basis of morphological studies. And it provides the link by which fossil material can be analyzed, and thereby permitting the incorporation of the extremely essential element of time into systematic studies.

Over the past two decades, a slow revolution in morphological studies has occurred, of which the rise of functional morphology is only a part, and has led to a broadly based discipline that may be called "evolutionary morphology." In brief, evolutionary morphology is the comparative study of the biology of mophological features in accordance with the principles of evolutionary theory. Evolutionary morphology is comparative anatomy catching up with the New Systematics.

I will cover two topics. First, I will consider approaches to systematics of the higher categories, this being the area of morphology in systematics. In all cases, when I say systematics, I shall refer only to systematics on the generic and higher levels. And second, I will consider methods of morphological studies. My discussion will apply equally well to recent and fossil organisms; the method of study of fossil organisms does not differ in any significant way from those used in studying recent organisms. The only real difference is that the study of fossils is far more difficult and yields considerably less morphological information. Much of this discussion is based upon a recent talk (Bock, ms.)

Homology

Homology is the basic concept in the comparative study of any biological feature, and is one of the most misunderstood concepts in biology. It is important because comparisons will be meaningful only if properly comparable (= "the same") features are considered. It is also important because the names of morphological features are based upon homologous features and the same name theoretically can be applied only to homologous features.

Before attempting to offer a definition of homology, I would like to comment briefly upon the nature of defintions. A definition is a theoretical concept, it defines a word. A definition does not, or does not have to include, the methods by which one recognizes objects to which the definition applies. After a defintion has been formulated, then a set of methods must be established by which one can recognize objects to which the definition applies. In offering the following defintion of terms, I will keep the defintions and the methods for recognization absolutely separated. It is also possible to offer operational defintions which combine both

aspects. The approach of operational defintions is a perfectly valid philosophical approach, but it is not the only valid method as claimed by certain systematists.

Homology is only meaningful if it is based upon the fact and consequences of organic evolution. I would reject any other definition of homology. Hence, the only meaningful definition is one based on evolution, that is, a phylogenetic defintion of homology (Bock, 1963); namely: "Homology: Homologous features (or conditions of the features) in two or more organisms are ones that can be traced back to the same feature (or condition) in the immediate common ancestor of these organisms." Contrary to a commonly held belief, this is not a circular definition. Nothing has been said about the methods by which features are judged to be homologous; these will be discussed below. Homology is not an intrinsic property of features. It is not something like mass or color, but it is a relative property depending on the existence of features in other organisms. The defintion of homology just given applies to all features of organisms. It can apply to morphological structures, it can apply to behavioral features, it can apply to functional properties. The notion that homology applies to structural features and that analogy applies to functional properties is quite naive and misleading.

The opposite of homology is best called nonhomology and may be defined as: "Nonhomology (frequently called analogy): Nonhomologous features (or conditions of the features) in two or more organisms are ones that cannot be traced back to the same feature (or condition) in the immediate common ancestor of these organisms." Nonhomology is frequently called analogy as I have advocated in an earlier paper (Bock, 1963). However, it is probably better to use the homology-nonhomology dichotomy and eliminate the use of analogy altogether.

Two points in the definition of homology must be noted. First, no mention of similarity exists. The degree of similarity between features has nothing to do with the defintiion of homology. Second, nothing is said about embryological development, an aspect which is frequently included in the definition of homology. Use of the term homology to conote similar features is wrong and should be discouraged.

Statements about homology must always be put into the proper form. For example, one can say that the wing of a bat and the wing of a bird are homologous as the vertebrate forelimb. Or one can say that the flipper of a whale and the flipper of a shark are homologous as vertebrate limbs. The condition of the homology must always be given. The statement "The arm of the gorilla and the arm of the chimpanzee are homologous." is absolutely meaningless. The conditional phrase given the condition of the homology must always be included.

One of the vague points in the definition of homology is the exact definition of common ancestor. How closely must the common ancestor be given and what must be the condition of the feature in the common ancestor. Must the common ancestor be a single species and must the feature in the common ancestor be exactly like that in the descendent forms. This problem can be examined best in taxa containing numerous, morphologically similar forms, such as birds (see Bock, 1963, for examples). Analysis of these examples allows the conclusion that homology (or ar least recognizable homologies) is not an all or none concept; features are not either

absolutely homologous or nonhomologous. A gray area exists between unquestionably homologous and unquestionably nonhomologous features. This relative notion of homology corresponds to the relative notion of momophyly as discussed by Simpson. The degree with which homology can be recognized depends upon the uniformity of the taxa. And it should be noted that most higher taxa are the most uniform at the time of their origin. Hence even in heterogenous taxa, features that appear to be unquestionably homologous may have arisen several times in different members of a more uniform ancestral group.

The methods by which features are recognized to be homologous are varied. These methods must be, at least, in agreement with the general principles of evolution. They must no, of course, be based upon the presumed phylogeny of the particular group of organisms. None of the criteria used are absolute ones, all contain serious defects. Moreover, no one can prove homology with 100% certainty. The conclusion is always a probability statement which can never be proven. But these judgments must never be based upon the presumed phylogeny of a group -- the phylogenies are based upon the homologies.

The proper sequence of study and conclusions is most important. Features are studied first and their homologies established. That is, decisions must be made on homologous features in different organisms; these decisions are reached on the basis of criteria that will (hopefully) give accurate answers. Once decisions are reached on the homologies of features, this information can be used to deduce the probable phylogeny of the organisms. This sequence of study must be followed for the study of recent and of fossil organisms. The student of fossils obtains only the characteristics of the organism and its relative postition in time; from his material; he must establish any phylogenies in exactly the same manner as the student of recent organisms.

Hierarchical series of homologies may be established by formulating ever more precise conditional phrases about the possible homology and testing whetherthe features are still homologous. Once a hierarchy of homologies has been established this hierarchy can be used for establishing a hierarchy of relationships of the organisms which can be expreseed either as a formal classification or as a diagram of the presumed phylogeny or both.

Once homologies are established then the same name can be applied to this series of features. Presumably, the use of the same name for structures in different organisms implies that these structures are homologous. Herein lies a major problem in the use of earlier morphological literature, especially for the systematist who is not a morphologist but who must use morphological data. Numerous examples may be cited where the same name has been applied to nonhomologous features, often in the belief that the features are homologous. This danger becomes progressively greater in the older literature. Unfortunately no simple rules can be formulated for the detection of these erroneous uses; the worker must reevaluate each case morphologically, which may not be possible for many taxonomists. A real impass exists at this point because many taxonomists are not trained morphologists, yet must use morphological characters and still cannot offer their lack of morphological training as an excuse for repeating errors in the literature. My only suggestion is to be clearly aware of the difficulties in using morphological data and not to fall into the false security expressed by naive statements as "Anyone can compare morphological features."

Functional Morphology

Perhaps the most important advance achieved in morphology during the last decade is the widespread inquiry into functional aspects of morphological study. A knowledge of functional morphology has allowed a far greater appreciation of the taxonomic value of these characters. The acknowledged importance of functional studies has many inherent disadvantages resulting partly from a lack of a proper set of defined terms and partly from inadequate training. Little agreement exists as to what sort of studies are done in dunctional anatomy, what can and what cannot be done, how functional morphology may differ form what may be called biological morphology, ecological morphology, and so forth. Terms such as function must be clearly defined because they have been used in several quite different ways in the literature. It is almost impossible, for example, to know what is meant by the statemtnt "The function of a feature cannot be deduced from a study of its morphological form." This statement can be correct or wrong depending upon which of the two commonest usages of function is meant. The statement that "In evolution the form of a structure changes first followed by a change in its function" is either correct, incorrect, or quite meaningless depending upon the meaning of function.

In an attempt to clarify some of the problems associated with the terms function and adaptation, von Wahlert and I (1965) offered definitions for a set of interrelated concepts. These are quite formal defintions and form an internally consistent set; they are not the only possible set.

The feature of an organism is the attribute about which one is speaking, and can be defined as: "Feature: Any part or attribute of an organism will be referred to as a feature if it stands as a subject in a sentence descriptive of that organism." Nc attempt should or can be made to delimit "unit features". Also it should be noted what may be reasonable morphological features does not have to coincide with physiological, developmental, or genetical features.

The form of a feature includes the material comprising it and how it is arranged, and may be defined as: "Form: In any sentence describing a feature of an organism, its form would be that class of predicates of material composition and the arrangement, shape or appearance of these materials, provided that these predicates donot mention any reference to the normal environment of the organism." One of the important parts of this definition is the concept of organization -- how the material is put together -- which will be significant in later definitions. It must be noted that a feature does not have to have a single form as commonly implied by morphologists. The form of a feature may change over a period of time, often over a very short period. The form of a muscle changes as it shortens, the shape of the lens of the eye changes, the shape of the intestine changes depending upon the amount of food it contains and so forth. Teeth wear, avian feathers bend because of air pressures. These differences in shape become quite important so that the morphologist must be aware of the possible spectrum of forms that a feature may possess.

The function of a feature is what the feature can do depending upon its form and can be defined as: "Function: In any sentence describing a feature of an organism, its functions would be that class of predicates which include all physical and chemical properties arising from its form

(i.e., its material composition and arrangements thereof) including all properties arising from increasing levels of organization, provided that these predicates do not mention any reference to the environment of the organism." In accordance with this definition, most, if not all, features have a number of functions. This is especially true if the form of the feature varies as in the case of muscles or the lens of the eye; as the form changes so does the function. Moreover the functional properties depend upon the organization of the material and upon the exact organization in increasing complexity. Many of the functions may be unutilized ones and some may be biological nonsense. But they are all valid functions. The most important aspect of this definition is that the environment of the organism is excluded. Hence functional studies are ones that can be done in the laboratory without consideration as to the biological significance of the particular functions.

The combination of form and function may be termed the faculty and defined as: "Faculty: A faculty is defined as the combination of a form and function of a feature. In any sentence describing a feature of an organism, its faculties would be that class of predicates each of which includes a combination of a form (material composition and arrangement) and a function (physical and chemical properties) of a feature, provided that these predicates do not mention any reference to the natural environment of the organism." A feature has as many potential faculties as it has forms and functions; many of them are unutilized ones depending upon the functions. The faculty is the key to understanding adaptations because it includes both the formal and the functional properties of the feature. It should be obvious already that this set of definitions eliminates such vague statements that the form of a feature is adapted to its function.

The biological role of a feature is what an organism does with its features during its normal life history and can be defined as: "Biological role: In any sentence describing a feature of an organism, the biological roles would be that class of predicates which includes all actions or uses of the faculties (the form-function complexes) of the feature by the organism in the course of its life history, provided that these predicates include reference to the environment of the organism." The only way that a biological role can be determined is to observe the organism living normally in its environment. If an animal has a series of morphological features that allows it to run in a certain way, then we know only its functional properties and not why the animal possesses these properties. In ascertaining the biological role, one determines whether the animal runs to escape from a predator, or to catch its food, or to locate potential mates and so forth. In the study of biological roles, the organism must be studies in its normal environment; here is where morphology, ecology, and animal behavior meet. Most important is the inclusion of the environment in the study which is the basic distinction between the study of fucntions and of biological roles.

I will maintain that given a proper knowledge of how morphological features work, sufficient deductions about their functions can be based upon a knowledge of the form of the feature. This is very important because if one knows the correlation between structural and functional parameters in muscles, on can then dissect the muscles of animals which cannot be studied in the laboratory and make reasonable statements about their functions. If one knows how bones operate, how forces act and how forces are distributed within bones, then with the help of free-body

diagrams and other techniques, considerable knowledge can be gained about the functional properties of fossil organisms simply by knowing the morphology and the correlation between structural and functional parameters.

Although it is possible to deduce the functions of many features of organisms that are not readily maintained in the laboratory, deductions about biological roles cannot be based with any certainty on the study of only the forms and function of features. Herein lies the major problem of trying to know what an organism does with its morphological features and to deduce adaptive significances. This problem exists for recent organisms and becomes especially acute for fossil forms. Examples illustrating this problem of morphological analysis may be found in any text.

Work in functional anatomy is hindered at the present time by a lack of comprehension of the pertinient problems to be tackled and by a lack of knowledge of the approaches that can be used to solve the problems at hand. And especially, functional anatomy is being hampered by a sadly insufficient amount of experimental work. Although these are major problems at the present itme, they can be solved and much work is being done at this time along these lines. Much of this work is on the functional properties of the vertebrate muscle-bone system which is especially advantageous because most morphological features used in taxonomic studies are from the muslce-bone system. References to some of these studies may be found in the attached bibliography.

Adaptation

A few words must be said about adaptation as a basis to the important subject of how to treat adaptive features in taxonomy. The defintiions are taken from a study by von Wahlert and myself (1963).

After formulating a set of definitions about features, the environment must be divided into various components. The important defintions are:

"Habitat (Umgebung): The habitat of an organism is comprised of those factors of the environment which possibly could be utilized by that organism or which possibly could act upon that organism."

"Specific-specific habitat (UMwelt): Those factors of the environment which are actually being used by the orgainsm or which are actually acting upon it comprise the umwelt or specific-specific habitat; the organism must be present to recognize the umwelt."

"Selection force: A selection force is a factor of the umwelt that interacts with the organism and in particular interacts with the faculty of a feature through its biological role."

"Selection: Selection is the action of any factor of the umwelt on an organism through the appropriate synerg that results in a non-random differential reproduction of genotypes."

"Synerg: A synerg is the link between the organism and its umwelt formed by one selection force of the umwelt and one biological role of a faculty."

"Niche: The niche of an organism is the sum of all of its synergs; thus it is the total relationship between the whole organism and its complete umwelt."

The greatest problem in this set of definitions is the use of the term niche which has been used for what I would call the umgebung, the umwelt and the niche. No matter what terms are used, this set of definitions are needed. The slight difference between the defintiion of selection force and selection is of little importance.

The concept of adaptation has always pertained to a part of the organism and always with respect to the environment. Hence the definition for an adaptation and measuring its relative "goodness" may be as follows:

"Adaptation (evolutionary): An adaptation is (a) a feature of the organism that has a role in the life history of the organism (i.e., must perform some definite task, such as obtaining food or escaping from a predator), and (b) perform this role with a certain degree of efficiency."

Hence, an adaptation is always part of the organism and is a faculty of a feature which has a biological role and interacts with some environmental factor of the umwelt of the organism. The bond between the faculty and the environmental factor is the synerg formed by the biological role interacting with the selection force.

"The degree of evolutionary adaptation, the state of being, is defined as the minimal amount of energy required by the organism to maintain successfully the synerg if a single biological role of a faculty is considered, or to maintain successfully its niche if the whole organism is considered."

"Evolutionary adaptation, the process, is defined as any evolutionary change which reduces the amounts of energy required to maintain successfully a synerg or the niche as the case may be, toward the minimum possible amount."

Adaptations must always be judged with respect to a previously stated environment. It is really only possible to compare different adaptations to the same environment, and makes far less sense to compare the relative adaptiveness of different adaptations each to its own environment.

For completeness, two more definitions should be given:

"Preadaptation: A feature is said to be preadapted when its present forms and functions allow one of the faculties to acquire a new biological role and hence establish a new synergical relationship with the umwelt whenever the need (= appearance of the selection force) for the new adaptation (the faculty) should arise."

"Adaptive features: Those features that are favored and maintained by selection are adaptive, by definition. Those that are rejected and eliminated by selection are non-adaptive."

Adaptive features and classification

In using morphological characters in classification, the old question of the value of adaptive characters must be answered. Many workers have claimed that adaptive characters are useless as taxonomic characters. Yet no morphological feature known to me that has been used as a taxonomic character has been proven to be inadaptive and many have been proven beyond doubt to be adaptive. Obviously, if adaptive features are not useful as taxonomic features one can ask what features of organisms are left for the

taxonomist to use in his work. A dilemma exists here, indicating that some error has been made somewhere.

I would advance the hypothesis that adaptive features may be extremely useful as taxonomic features; that is, that adaptiveness in itself does not negate the taxonomic value of the feature. The value of a feature as a taxonomic character depends on considerations quite apart from simply whether it is adaptive or not.

The basic consideration in support of this conclusion rests upon a clear distinction between evolutionary mechanisms and phenomena that are associated with the origin of new features and of their later modifications and those evolutionary mechanisms and phenomena associated with maintaining or selecting these features. The first set of mechanisms includes the formation of all genetical variations and other chance-based evolutionary phenomena. The secondary mechanism is that of natural selection. Both sets of mechanisms must be considered, not only selection as done all too often.

Adaptive aspects of a feature are the easiest to consider and may be defined as: "Adaptive aspects: Those aspects of properties of a feature that are responsible for the feature being favored by selection would be the adaptive aspects of the feature." Hence the adaptive aspects of a feature are responsible for it being favored by selection and hence being maintained. These aspects need only to lie within the limits set by selection as selection can only choose between features that lie within these limits and features that lie outside of these limits. Selection can only choose features according to a rather fixed interaction between the organism and the environment. Hence, selection and adaptation are the design aspects of evolution in the sense of Mayr, who has discussed the dilemma between the design and accidental causes of evolution.

But natural selection is no the only evolutionary mechanism controlling the evolution of biological features. While selection can choose or reject a feature, it cannot decide to reject an acceptable feature because it is not the theoretically best possible one; and it cannot predetermine the properties of the features exposed to it. The appearance of all features, their origin and the origin of all later modifications, lies outside the control of natural selection. This control lies under the control of chance based genetical processes that generate the genotypical variation underlying the phenotypical variation and other chance based evolutionary phenomena. The aspects of a feature under the control of these evolutionary phenomena may be called paradaptive aspects and may be defined as: "Paradaptive aspects: Those aspects or properties of a feature that are dependent upon, resulting from or under the control of chance-based evolutionary mechanisms are the paradaptive aspects of the feature. Paradaptive (from "para" and "adaptive" meaning "besides adaptive") aspects are not dependent upon selection and hence cannot be judged in the range of adaptive to nonadaptive." The important property of the mechanisms and phenomena controlling paradaptive aspects is that they are chance based with respect to the demands of selection and with respect to future selection forces and future evolution of the feature. These factors constitute the accidental aspects of evolution in the sense of Mayr.

The essential attribute of paradaptive aspects of features is that their occurrence is chance based and thus the chance that a particular paradaptation will appear depends upon the probability of its occurrence.

All aspects or properties of a feature are simultaneously paradaptive and adaptive because they have originated and, presumably, have been favored and maintained by selection. Paradaptive differences are associated more with horizontal comparisons and adaptive differences are associated more with vertical comparisons. These two types of comparisons, important to systematic theory, may be defiend as: "Vertical comparison: All comparisons between members of the same phyletic lineage, between ancestral and descendent groups, are vertical ones." "Horizontal comparisons: All comparisons between members of different phyletic lines, no matter whether or not the organisms exist at the same time level, are horizontal ones."

Classification is essentially the distinction between monophyletic (vertically based) groups of organisms. As such, classification is the distinction between gouups of organisms possessing different paradaptive properties of taxonomic characters. Paradaptive properties of features, being associated with the origin of features, will also be associated with the origin of taxonomic groups. Thus a study of paradaptations would provide a good guide to the existence and limits of groups of organisms. Hence it is the paradaptive aspects of features that are important for the taxonomic value of these features.

If the paradaptive aspects of a feature determine its taxonomic value, what determines the taxonomic value of paradaptations as it should be immediately obvious that not all paradaptations have the same taxonomic value. The significant difference between different paradaptations is the probability of their occurrence and this difference is of paramount importance for the evaluation of their taxonomic value. The probability of unique occurrence of a particular paradaptation in the evolutionary history of a group of organisms would vary from very low to very high. Those paradaptations with a high probability of unique occurrence would have great taxonomic value and those with a low probability would have little taxonomic value. The methods for evaluating these probabilities are only being developed now. All that can be offered now is that the paradaptive aspects of taxonomic features can be ascertained only after the adaptive aspects are known, and this work depends upon sound functional morphological studies.

Conclusions

The ideas presented in this paper are only a fragment of those being tested in recent morphological work. The emergence of evolutionary morphology is establishing a more sophisticated theoretical foundation for systematic study of the higher categories with the clear realization that these studies are not simply a comparison of the similarities of the groups under consideration. With the available wealth of comparative information, the ease of storing material and the only available direct key to fossils and the essential element of time, and with the impetus being generated by the emergence of evolutionary morphology, it may be predicted that morphology will long remain a major cornerstone of theoretical and practical studies of biological classification.

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DISCUSSANT

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I think insects offer a great deal toward some phases of biology, as far as the future and prospects of functional morphology go. Entomology has a long way to go because there are so many different types that we haven't discovered yet, and any entomologist working on a large group can certainly state many instances where he is describing new forms that add greatly to his overall knowledge, both on his morphological definitions and on his behavioral definitions or characteristics of a group. The morphology of the insect head has been studied as far as basic parts go, but we still don't know the full range between species and genera and so on. This is unfortunate because I think that the study of the insect head will lend a great deal of knowledge to some of these statements which have been made so far today. If you compare the basic biting-type, chewing-type mouth part as you find in Orthoptera and follow this up through some of the numersteoid groups such as Lepidoptera, you find a very great modification here, greater than that which you have encountered in all the vertebrate classes.

We have not talked much about the appearance of new structures. This is something that is difficult to show because we do not have enough information. In the yucca moths, you have an appearance of the structure which now has no antecedent. We refer to this structure as the maxiloid tentacle. Its biological role is to manipulate pollen, and it does this very deliberately, forms a mass under the head, transports this pollen to the stigma of the flower, and actually rams this pollen down into the stamatic tube of the yucca plant. I have investigated many types of insects to try to find some antecedent to this particular structure. It arises from the basal segment of the maxillary palp. I have looked at orders other than Lepidoptera and so far have not found anything which is even remotely similar to it....

ANIMAL BEHAVIOR AND SYSTEMATICS

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Introduction

I have thought about this lecture all the way down here, and I still cannot imagine that at eleven thirty I'm still going to be standing here talking and you're still going to be sitting out there listening! I have never talked for two and a half hours straight. I have always thought I was pretty lucky in teaching if I got fifty minutes ahead of the students, which is an absolute minimum. Furthermore, I realized on the way here that I couldn't think of anyone that I would like to listen to for two and a half hours!

After having these thoughts, I decided to make some changes in my talk. The principal one is that it is really going to be a series of short talks, each ten or fifteen minutes long. I'll try to pause between these for questions and I hope that you'll also interrupt me at any time you want.

I don't know most of you, and I don't think that most of you know me. My topic is supposed to be animal behavior and systematics. I decided that staying precisely with that subject is probably the least important thing I can do. Instead I will try to emphasize those things in which I at least feel that I have some special competence or special information. It seems only fair, therefore, that I should tell you a bit about my background so that you'll understand how I happen to be here, and why I tend to emphasize the things I do. I got a degree in entomology at Ohio State University, where I became a systematist more or less indirectly through the influence of my advisor there, Donald J. Borror, and also because of a paper on cricket speciation that I read in my early graduate student days, written by Bentley B. Fulton of North Carolina State University. I spent my graduate student days proclaiming that one place I would never be found working is in a museum. But then I left Ohio State, went directly to work in a museum, and have been in a museum ever since!

In the United States, animal behavior was almost non-existent as a subject in zoology curricula in the early 1950's. Partly as a result, I nearly became a psychologist. But somewhere along the way I got diverted into biology. When I went to Michigan I taught introductory zoology for five years. My interest in animal behavior grew during this time, and I eventually started teaching a course in insect behavior and a graduate seminar in evolution. Finally these two courses became combined into a course called animal behavior and evolution, which I have been teaching the past four years.

So I am really a systematist with a special interest in behavior, and I'm still studying the same insects that I started to work on as a graduate student: the crickets, katydids, and cicadas--three families containing about a thousand species in North America. My chief ambition at this moment is to finish a monograph on these species, along with Thomas E. Moore at The University of Michigan and Thomas J. Walker at the University of Florida.

If I have any special knowledge about behavior, then, it is a result of coming in more or less through the back door. I am quite serious when I express the hope that Dr. Eisenberg, who did not come through the back door, but, more recently than I, through one of the big open front ones, will not hesitate to straighten out any important errors that I might make.

Some General Comments on Classification

First, I want to give a brief discourse on something I got to thinking about as a result of the systematics conference we had at Ann Arbor three weeks ago, and which has only a very indirect relationship to behavior.

I consider myself a systematist and a taxonomist--in both the broadest and narrowest senses of those terms. I mean by this that I am not willing to admit that taxonomists engage in any worthwhile activities that I don't carry out in my own biological work. I don't claim the same for systematics in the broadest sense, but at least I do believe that systematists, collectively and individually, are not likely to be interested in anything in biology that is not directly of interest and concern to me too.

Nevertheless, I am one of those many taxonomists, or systematists, who never has worried too much about higher categories. I think I always have had some sort of vague feeling that when the proper time arrived, or when the necessity of dealing with them became sufficiently urgent, they would either fall into place or I could at least work something out on a provisional basis.

I have been noticing, of course, the steady increase in the number of papers dealing with the arrangement of higher categories, particularly those published in Systematic Zoology, and, I might add, the steady increase in the complexity of their discussions; and I include in this growth of complexity the writings and suggestions of philosophers, logicians, statisticians, and numerical pheneticists (whatever they may be).

But I stopped trying to keep up with these papers because I never could develop the intensity of concern I seemed to need to go to the trouble of trying to understand all of the arguments. I think I have had some kind of sneaky hope that these people would argue around among themselves until they figured it all out, and then I could just read the summary!

After I had sat through the first day or two of the Ann Arbor conference, I was actually beginning to wonder if I am a systematist after all! Because here all of these people were, right in front of me, arguing the same issues vocally that I had been sort of skipping over when they were published in Systematic Zoology and other journals. I might add that a lot of other people to whom I talked were also wondering out loud if they were systematists. This made me feel a little better.

As I listened, it struck me that there were two kinds of people present at that conference: first, those behaving as though classification is something you do so that you can proceed with biology--or even something that you do more or less independently of the growth of biological knowledge in general; and, second, those who act as though they believe that classification is something that proceeds out of biological knowledge in general, or is possible as a result of the general growth of biological knowledge--something that is dependent upon general biological knowledge, contributes directly to it, and in fact is involved in a kind of reverberating feedback with it.

The first category includes some investigators that all of us would call the old-fashioned variety of taxonomist, and some who are bound and determined, it would seem, to think of themselves as the most new-fangled of all taxonomists.

Someone in a discussion following the conference asked a question that I think ultimately bears on my feeling that there are two kinds of people talking about classification. He said, "Well, why do we need classification anyway?" What struck me from the answers he got immediately was that when you start listing reasons--say, you need classification for biogeography, for understanding evolutionary mechanisms, for working out geological history, or for understanding the evolution of some particular characteristic--then you begin suddenly to realize that all of these reasons are not equally urgent at any stage in the development of biology. Furthermore, classification at the different levels in the taxonomic hierarchy does not contribute equally to these different problems to which classification in general contributes.

And so, the question, "Why do we need classification?" suddenly becomes "How much classification do we need when?" Someone suggested that some of the numerical pheneticists saw a lot of taxonomists behaving as though they wanted the "complete and correct" classification right now, said, in effect, "Oh, if that's what you want, I can show you how best to do it!," did it, and cannot figure out now why the systematists don't really want the technique.

The reason, I think, is that a classification is not something that one sets up completely so that he can then proceed with the rest of biology. It is something that, at first, in its most provisional, rudimentary state, assists beginning efforts toward the collection, arrangement, and understanding of biological information, and thereafter is alternately adjusted and refined by, and then used to test the significance and validity of, biological information of all kinds and in all stages of development. It is something that contributes continually to the growth of biological knowledge in general and yet can never be complete as long as biological information is still coming in. This is why the systematist, at his best, has to be not only the chief pioneer in biology but as well one of the ultimate synthesizers.

I have been wondering since that meeting if it is not possible that lack of agreement on this point underlies every major disunity in systematic biology? And that failure to understand it, or agree with it, is responsible for many of the trivial, inadequate, and mis-directed efforts in systematics? I include here those people who, when involved in some big biological project, go out and "hire" a taxonomist--and who then take the taxonomist's word as gospel on classification and work everything else around what he says, not realizing that every piece and kind of biological information they discover is also taxonomic information.

Construction of a classification, then, does not proceed independently of the growth of biological knowledge in general; indeed, it must neither run too far ahead nor lag too far behind the development of other aspects of biology. But how do we decide what is "too far ahead" or "too far behind?" I think we do it by asking again that same question: "What do we need classication for?"

Classification at any level or in any group might be construed to have "fallen behind," hence, deserve more effort (Could we say that special effort toward it would be more rewarding, useful, and effective?) when its absence or its imperfections are retarding progress on questions pertinent to the groups of organisms or the evolutionary events involved.

Adequate classification is not going to proceed on its own. On the other hand, is it not possible to work so hard at classifying at any point in the development of knowledge about a given group (or at a given level in the classification hierarchy) that the effort necessarily will be trivial? Is this perhaps a part of the background for the exaggeration of efforts at weighting and selecting "characters'? Don't the relative costs of these efforts increase with the intensity of efforts at classification relative to the extent of biological information available?

The "level" of classification" which comes closest to being justified regardless of what else is known is that "level" needed for identification or repeatability which, of course, is the essence of science. Most often this is the one we call the "species." This is especially true, and easy to understand, when the species has what we call the "biological" meaning--or is clearly synonymous with the smallest, or most truly separate evolutionary line--in at least bisexual organisms.

I have sometimes believed that some of the decriers of the biological species concept have just been unable to figure out what species are in their groups, and they'll be damned if they're going to let anybody else think he's done it in his group!

But, look how inappropriate, in this light, is the idea that "species" don't have to be biological species even when they can be! I'm referring now to the idea that one can handle this level of classification without dealing with biological entities--that he needs only to identify groups of look-alike specimens. I would ask those people who challenge the biological species concept whether they do not need it as badly as some of us who are convinced that in our organisms we can cause it reasonably to represent the forking of the phylogenetic tree--the origin of discontinuity? I would ask them if they are sure they have not been using it all the time as a standard against which to compare and understand their own organisms when they may think don't evolve that way at all? I agree that it is unfortunate that populations of asexual and parthenogenetic and other non-bisexual organisms have not been studied enough to understand the significance of their similarities and differences, cohesiveness or lack of it; but I do not think we should blame the biological species concept for this particular area of ignorance, or do away with it because we don't know whether or how universally it can be applied.

I think we need to find "biological" species wherever they exist, and perhaps we need to find distinct evolutionary lines as analogous to biological species as they may be, in all kinds of organisms.

But, going back to higher categories, we really don't need the family as badly as the species, nor do we need, say, that badly the order or the tribe. Perhaps we ought to talk about degrees of antiquity rather than taxonomic levels: in general, the more recent the evolutionary divergence, the more likely we are to need the classificatory effort at that level earlier in the growth and development of general biological knowledge concerning that group.

If I can inject one more comment on this general theme, I have been serving on a panel on which we have been admonished continually to "describe the problem-solving methods of your field." At first I didn't really think this assignment was appropriate with regard to systematics, but I finally decided it is a very valuable one. For one thing, pondering it caused me to realize that in a field with as much history as biology, classification itself is one of the most crucial problem-solving methods! I'm sure that many of you already know this, and you may have specific and personal examples to demonstrate it. But let me explain what this remark means to me, for I feel that I have only recently become aware of its real significance.

A couple of weeks ago, I found myself explaining to a novice that two look-alike Gryllus species with quite different chirps are "not even in the same species group." Suddenly, my own remarks caused me to realize that all of the field crickets of North America (about 40 species) fall into just three species groups. This realization caused distributions, habitats, life histories, behavior, and morphology to fall suddenly into place in my mind. What had been a confusing tangle of data became an orderly, reasonable, exciting story, and partly as a result when Ashley Gurney (sitting in this audience) next asks me: "When are you going to finish the field crickets of North America?" I think I can say "Right away!"

As soon as I gained the realization of species group identities, I knew that if my idea was correct then certain subtle morphological differences ought to exist between the two specimens I was holding. Each was present: (1) more pubescence on the head and pronotum of one cricket, (2) a bigger head on the other, (3) a more prominent light line along the tegminal margin in the first cricket, (4) tan spots on the inside of the hind leg of one cricket and orange or reddish ones on the other, and (5) certain subtle differences in body shape and wing glossiness. Yet I noticed none of these differences until I had placed the crickets in different species groups by their songs--going a little beyond my own inclinations because I was trying to explain something to a novice and was exaggerating somewhat to make a point. Here I must acknowledge that my classification of field crickets needed to "catch up" with my general information.

I ought to point out here that what I had done in this case was something that everyone insists cannot be done: I was, in effect, using a reproductive isolating mechanism (song) to classify "higher" categories (species groups). I want to come back to that after discussing reproductive isolation a little more thoroughly, and argue that the people who say you can't use reproductive isolating mechanisms to group species into higher categories are misleading biologists in a very important way. They are right in the sense that the differences actually responsible for reproductively isolating particular pairs of species must usually be of recent origin, and change must be rapid in such characteristics. They are wrong in supposing that there are not some features of such phenomena which do not change rapidly. A cricket song, for example, is not one character--it is a whole constellation or hierarchy of characters, some of which are not any longer changing with every case of speciation; and some of which reveal generic and even subfamilial relationships. Part of the reason for the evolution of hierarchial complexities yielding such useful characteristics is that speciation and reproductive isolation force species specificity

and overall rapidity in evolutionary change. I will give an example when I take up reproductive isolation later this morning.

The History of Behavioral Study

I doubt that any area or field within zoology has had a more curious history than the study of animal behavior. None of the characteristics of animals are more broadly interesting than those which we lump under this term "behavior," and there is ample evidence that men have been intensively preoccupied with behavior, and skillful interpreters of it, for many thousands of years. Nevertheless, throughout the history of zoology as a formal discipline there never has been a very long period during which behavioral study was able to maintain a consistent respectability. At times it has seemed that the mere acquisition of formal training in zoology was almost synonymous with the suppression of any active interest in behavior. No field has seemed more devoid of a cumulative growth of knowledge, and it is not surprising that in the early part of this century the zoologists more or less just gave up and turned the entire subject over to the psychologists. As recently as 1956, when I was still a graduate student, it was virtually impossible to obtain a Ph.D. in this country with animal behavior formally given as a major field of concentration. There was a mere handful of courses concerned with behavioral topics. In zoology, they were practically all moribund hangovers from the old "anatomy and development" themes of the 1930's, and in entomology they were almost exclusively concerned with social life in ants, wasps, bees, and termites.

This has always been a most puzzling phenomenon to me, because I have been impressed with the idea that "behavior" is almost a part of the definition of "animal." Is there anything that more clearly sets animals apart from plants than the evolution of complexity in behavioral phenomena? Anything that more clearly analogizes on a broad scale the independently followed evolutionary pathways of such anciently divergent animal groups as the vertebrates, the molluscs, and the arthropods?

I was reminded of the attitude toward behavior that I have been describing only last week when I gave to a taxonomist a copy of a key to the flashing patterns of the 13 species of fireflies flashing right now in the swamp behind his house, a key made up by James E. Lloyd of The University of Florida. In the first couplet, the genera Photuris and Photinus are distinguished, and in addition to color of flash and the behavior of captured males in one's hand, Dr. Lloyd included the difference in striping on the elytra. This zoologist's only remark about the key was a somewhat triumphant one to the effect that he noticed that morphology "had to be used" in the very first couplet. He had already forgotten the main reason that I gave him the key, which was that one year before he had told me that there were only three species of fireflies in his swamp!

Behavioral Study and the Development of Zoology

When men began formally to study animals, they started with anatomy, in the contexts of medicine and classification (or taxonomy). At first the mere acknowledgment that an animal can be divided up into namable parts or units (descriptive, gross anatomy), the study of anatomy became comparative with the realization of similarity, which in turn led to the development

if not the immediate distinction and clarification, of the concepts of homology and analogy.

Anatomy, or morphology, is quite a different thing from behavior. It is something that is permanent, not fleeting. You can study it, think about it, draw pictures of it, and write about it; and all the time it stays there in one place so that you can check and re-check whenever you wish. One man could easily check another's results, and individualistic interpretations were not so easily defended. A true accumulation of knowledge could take place.

Anatomy has continued as a basic form of study in zoology for the reasons that (1) it has become increasingly repeatable (with better methods of preservation) (Repeatability, you will note, is at the heart of what has been called the scientific method, (2) it has been subject to finer and finer analyses (with the development of better and better microscopes), and (3) it forms the best link with past, extinct life through fossil remains.

The early anatomists seemed principally to be interested in animals similar to man, and the rise of medicine is intricately involved in early anatomical work. A second great usefulness appeared when Linnaeus developed his system of classifying and naming animals and plants, using principally structural or anatomical features that he could describe from dead specimens. Linnaeus never travelled far from the place of his birth, but he named thousands of animal and plant species from the far corners of the earth--brought to him dead and in various stages of preservation and decay.

With the rise of morphological study and the desire to classify and arrange the animals of the world, came the museums--places to store collections and type specimens. With the rise of museum work came the museum "expeditions"--trips by groups of collectors with the goal of bringing back well-preserved specimens of every animal species possible. The success of the trip was measured by the number of specimens brought back, for amount of information were usually equated with numbers of specimens.

On such expeditions, little or no time was spent observing the activities of animals--such things as how they lived, what they ate, or which ones mated with one another. Time taken from collecting was time wasted, and to take the chance of losing a specimen just so you could see what it was going to do next was considered to be a blunder of considerable proportion. The locality was recorded, often in a most exact and detailed fashion, so that later expeditions could come to exactly the same spot if they wished to check on a particular specimen. Still later, it became evident that the habitat of a specimen was important in determining its identity and the significance of finding it in a particular place. Long lists might be made of the plants and animals noticed where a particular species was found--especially if it looked like a new species. The studies of zoogeography and systematics--where animals live, how they got there, and how they are related to each other--were developing together.

Still more recently, biologists have become increasingly aware that the activities of species are often the best clues as to their distinctness and their relationships with one another. Frog calls, firefly flashing

rhythms, bird songs, butterfly flight patterns, moth odors, ant swarms, dragonfly territorial flights, and cricket chirps are samples of the kinds of behavior that taxonomists have found to be important in identifying and classifying species. But not until recently have taxonomists been willing to admit that they use such things in taxonomy. B. B. Fulton, the man who originally inspired me to work on crickets, wouldn't describe his new species that he found by their chirps. He told me he 'didn't want to incur the wrath of the museum taxonomists." Although he, W. S. Blatchley, and Harry A. Allard are the only old-time North American orthopterists whose work stands with few or no alterations, none of the three, except probably Blatchley, considered themselves systematists, and neither did the "professional" orthopteran taxonomists.

When I have used a tape recording to plot distributions, I have on occasion been challenged by fellow taxonomists who ask me "Where is the specimen?" I say that the tape is the specimen, but this is not satisfactory. Why is a piece of a carcass more adequate than a song record? Each is a part of the animal's phenotype, and each is subject--perhaps equally subject--to errors of labelling and identification.

Recent increases in emphasis on the nature of animal activities have brought about startling changes in the activities of taxonomists. Less time is spent making exhaustive analyses of the measurements of dead specimens or skins, and more time is spent recording and describing what the animals do while they are alive. Biologists on expeditions for museums sometimes are as frequently found studying the activities of their animals as they are actually collecting or preserving them, and when they return from the trip their principal loads sometimes are cages of live animals. Taxonomists have been assisted in this important shift in their activities by the development of some really important tools. Complex photographic equipment, high fidelity portable tape recorders, and other means have been developed for preserving behavior patterns for later analyses and comparisons. One of the most dramatic of such tools in my experience is the electronic "eye" that Jim Lloyd can point at fireflies in flight and obtain a tape-recorded beeping pattern corresponding to the flash pattern, set at any frequency he desires. Remarkably effective methods for keeping animals alive in the laboratories, observing their activities, and hybridizing different species have been developed. Perhaps most important of all are the modern means of travel available to taxonomists. No longer must they rely upon the whims of wealthy explorers or the occasional, laborious, and unwieldy expedition. A New York biologist with special interests in a group of animals in Trinidad can step aboard a jet plane and be out in the field hard at work in a few hours. Taxonomic biologists can be found in all parts of the world. I happen to believe that the days of proxy collectors are about over. Few top-notch systematists are going to settle for someone else sifting through the habitats where their animals live and bringing back the fragments they find.

Going back to the early days of formal zoology again, just as Aristotle's "body of facts" became more important during the early Christian era when authoritarianism was the sign of the times than the spirit of inquiry which developed them, so morphology, or anatomy, became, at times and to many biologists, particularly the taxonomists, more sacred than the repeatability originally responsible for its special value.

The study of anatomy has been followed by the development of a series of disciplines in biology that are well-known to all of us; descriptive embryology, physiology, genetics, and so forth. These are respectable portions of biology, well written up in all the introductory zoology textbooks.

But what has been happening to the study of behavior while all of this was going on? No one has ever denied that there is something definite called behavior, but, say, ten years ago, who had seen its history traced or its contributions welded into the developing pattern of zoology? A good argument can be made that it is the behavior of animals that characterizes them more than any other attribute--that, for example, sets their evolution off from that of plants. Why hasn't the study of behavior been at least cumulative enough to merit a tracing when zoological history is reviewed?

Actually, a variety of things had been happening to behavioral study during these first two centuries or so of zoology, and altogether they make a complex and interesting story.

A resurgence of anecdotal behavioral study occurred when Darwin's books were published. The idea of physical continuity inspired a search for mental continuity--evidence of "reason" in animals as well as "instinct" in man. Another began in the 1930's with the development of Lorenzian ethology, which we shall take up in some detail later.

C. R. Carpenter (1950:N.Y. Acad. Sci.) points out, with regard to the study of social life in animals:

"The prevailing 'climates of opinions,' including scientific value systems and attitudes of the majority of our research colleagues, are of such a character as to impose an unusual burden of proof on us for the professional status of our efforts and achievements. Those of us who are interested in comparative behavior, naturalistic behavior, and interactions of organisms are required to accumulate, and even dramatically to present, an overwhelming weight of evidence on very significant theoretical problems for these areas of research effort to be accepted and duly accredited. Our work is put into a disadvantageous position by the historic flood of poor natural history writings in our fields of interest. At the same time, the prestige of our work is not greatly enhanced by excellent qualitative writings during this quantitative-laboratory age."

Two nineteenth century trends in behavioral study were associated with anecdotalism, anthropomorphism, and natural history, which we ought to note. A strong feeling best termed anti-anthropomorphism set in in the late nineteenth century. Morgan's canon was illustrative of this trend; part of William Morton Wheeler's tirades were against it; Loeb's tropism theory, and the battle between mechanists and vitalists, carried on right up to the present arguments between people like Konrad Lorenz and Daniel Lehrman, and J. S. Kennedy and W. H. Torpe, are outcomes of it.

The connections with religious feelings and attitudes in behavioral study was not so surprising, for clerics worked hard to broaden the gap between man and animals, doubly so following the evolution backlash in post-Darwinian times. And underlying any evolutionary study of behavior is the eventual question of how man became a man, and in what way his mental evolution was a continuous process. One thing I must mention as an entomologist.

The entomologists never were too much disturbed by "anti-anecdotalism." They kept right on describing in detail how insects lived--species after species after species--but they called it bionomics, biology, life history, and almost anything but behavior. Fabre, Wheeler, the Peckhams, von Frisch, and many others--J. P. Scott (1958, Animal Behavior) a mammalogist, put it, "for a while social behavior was little more than a branch of entomology."

The Rise of Ethology

The development of the particular branch of behavioral study now known as "ethology" began to flourish following the Second World War, but it had its origins much earlier. One of the important individuals involved has been a German zoologist named Konrad Lorenz, who wrote his first influential paper in 1935, titled: "Der Kumpan in der Umwelt des Vogels" (The Companion in the Bird World). The ethological "movement" probably has to be described as the first sustained effort by zoologists to analyze animal behavior on a wide scale. The history of its development and its impact on psychology and zoology is both fascinating and instructive, and I am going to trace it here in some detail.

This story is one of the most interesting in all of biology because it has involved not only personalities and biological issues, but religious, philosophical, racial, political, and ideological differences as well. Perhaps it has revealed again man's inability to examine objectively the characteristics of animals that lie closest to the bases for his own ability to introspect and calculate and contemplate. In the history of ethology we will find, in succession, pre-World War II writings by a German accused of supporting Nazi views of racial superiority and of writing anti-semitic articles--more vehemently by a succession of Jewish comparative psychologists in America. A highly religious British zoologist has been accused, along with most of the other ethologists, by a British member of the communist party of being vitalistic, dualistic, and Freudian in his behavioral theories. I have said these things bluntly, but I believe there is something both surprising and enlightening about discovering how many of the emotion-provoking and even internationally critical issues of a few decades can be woven into a story of this sort--on the surface seeming to deal with a purely "scientific" subject, somehow removed from the problems of human relations. Perhaps, it only shows how inseparable are the study of man and the study of the rest of life--at least animal behavior.

The word ethology comes from the Greek word ethos. According to Mayr (In Schaffner, 1955), there are two Greek words which translate as ethos in English, one meaning "habit" or "custom" and the other meaning "character" (Mayr wonders if "ethics" did not come from the latter word). John Stuart Mill (1943) used the word to mean "the science of character," and A. F. Shand (1920) continued this use. But apparently the first zoologist to use the word to refer to animal behavior was our old friend William Morton Wheeler, who in 1903 wrote a paper titled: "Ethological observations on an American ant (Leptothorax emersoni Wheeler)," which he published, interestingly enough, in the Journal für Psychologie und Neurologie. Oskar Heinroth (1910) used "ethology" in a paper on ducks, and Lorenz then used it in his writings, probably causing the first widespread use of the term with his 1950 paper on "The comparative method in studying innate behaviour patterns." Lorenz himself has defined ethology as "that branch of research started by Oskar Heinroth." Thorpe (1961) says: "The word ethology in English

originally meant 'the interpretation of character by the study of gesture.' Some 35 or more years ago (1926[1]) it came into general use among zoologists to signify the comparative study and analysis of the instinctive or stereotyped movements of animals. It came to mean, in fact, the comparative anatomy of gesture of animal species. This zoological use was actually a narrowing from a wider scientific use prevalent in the early years of the century, when the term ethology was sometimes used to mean simply the scientific study of animal behavior. The present writer is convinced that this wide use is the right, indeed the only logical, use for today, and the term as so defined has great convenience for the zoologist as a complement to the term ecology."

One of the reasons that it is so difficult to give a discussion of ethology that will satisfy everyone involved is the intensity and emotionality of the arguments that have surrounded it since the Second World War. So many specific connotations have grown up around the word "ethology," and so many different opinions have been held by its proponents, that like comparative psychology it will probably be viewed by students in the future as another temporary sub-discipline in the study of animal behavior. If so, it will have failed in one way in the effort to bring behavioral study back to the zoologists, although, regardless of the name that zoologists choose to apply to this field (it is increasingly called merely "animal behavior," "behavior biology," or "behavioral ecology"), the ethological movement will probably have to be considered most important in its genesis.

It is possible to consider ethology in terms of:

1. the reasons for its appearance.
2. the methods espoused by its proponents
3. the neurophysiological, hereditary, developmental, and evolutionary ideas generated by it and attributed to it.

With regard to the first, I think we can say that the zoologists had begun slowly to realize that psychology, by splitting off entirely from biology and perpetuating itself solely through association with human pathologies and problems, had forfeited its chances of ever solving a significant number of the zoologists' problems regarding animal behavior. It had become not only largely non-evolutionary, but on occasion even anti-evolutionary.

It is not surprising that the ethological movement began in Europe. In America, comparative psychology was much more prominent than in Europe, where psychologists had concentrated more completely on the direct study of humans. One has to believe that the complexity of the methodological and theoretical aspects of comparative psychology in America has constituted a considerable deterrent to zoologists who might otherwise have become involved in behavioral study. Perhaps it is significant that the behavioral study of insects and other invertebrates didn't suffer from the same relegation to amateurs and anecdotalists that plagued vertebrate zoology in America during the early 20th Century.

I think Tinbergen's (1963) remarks describe well the effects of the continual frustrating drifting of zoology away from behavioral problems:

"One thing the early ethologists had in common was the wish to return to an inductive start, to observation and description of the enormous variety of animal behaviour repertoires and to the simple, though admittedly vague and general question: "Why do these animals behave as they do?" Ethologists were so intent on this return to observation and description because, being either field naturalists or zoo-men, they were personally acquainted with an overwhelming variety of puzzling behavior patterns which were simply not mentioned in behaviour textbooks, let alone analyzed or interpreted. They felt, quite correctly, that they were discovering an entire unexplored world. In a sense this 'return to nature' was a reaction against a tendency prevalent at that time in Psychology to concentrate on a few phenomena observed in a handful of species which were kept in impoverished environments, to formulate theories claimed to be general and to proceed deductively by testing these theories experimentally. It has been said that, in its haste to step into the twentieth centruy and to become a respectable science, Psychology skipped the preliminary descriptive stage that other natural sciences had gone through, and so was soon losing touch with the natural phenomena.

"Ethology was also a reaction against current science in another sense: zoologists with an interest in the living animal, overfed with details of a type of comparative anatomy which became increasingly interested in mere homology and lost interest in function, went out to see for themselves what animals did with all the organs portrayed in anatomy handbooks and on blackboards, and seen, discoloured, pickled, and 'mummified' in standard dissections."

I think that the principal reason psychology has not answered the kinds of questions that zoologists must have answered about animal behavior is that it was never comparative, and in general, it is not comparative now, in the zoological sense of involving the identification of homologies and the study of relationships among organisms. "Comparative" in psychology is very much like "comparative" in physiology has been: it involves comparison of selected types without any particular reference to the question of relationship. The phylogenetic variable is simply ignored.

Animal Behavior and Systematics

In 1905, four years after publication of De Vries' book, "The Mutation Theory," William Morton Wheeler delivered a lecture entitled: "Ethology and the Mutation Theory" in which, as he put it, he was "asked to consider the question as to whether the theory will apply also to the behavior or ethological, as well as to the morphological aspect of organisms."

Wheeler said several things in this paper that could have been said today, and I am going to quote a few of them, as illustrations of what entire lectures on the topic assigned me could be made up of. Ultimately I will get to what I think was the most important topic in his paper.

Wheeler said the following:

". . .in the field of possible observation the ethological tend to outstrip the morphological characters. We observe great differences in habits and behavior between genera of the same family, between species of the same genus, and what is most significant, between individuals and even twins of

of the same species. At the same time we may be utterly unable to point out the corresponding structural differences... . . It is clear that the prestige of morphology has been artificially enhanced by a continual appeal to complex invisible structures. . . . What bold man, for example, will undertake to show us the morphological characters corresponding to such striking differences in behavior as are manifested by the horse and ass, by cats and dogs of the same litters, or children of the same parents. . . ? Whatever may be the truth concerning such structures, it is undoubtedly a matter of considerable theoretical and practical importance that we are able to detect ethological where we cannot detect morphological differences or characters."

Wheeler is telling us systematists, students of diversity, that behavior is the most diverse level of organization in living things; that it is the most diverse level of expression of the phenotype. I would like to make an additional point. Systematists are concerned, not only with kinds of characteristics likely to reveal differences but also with those likely to reveal similarities, relationships, and common ancestry.

Although it may not seem obvious, if Wheeler is right, as I believe he is, and ethological characters do indeed tend to outstrip morphological characters "in the field of possible observation," then they should be more useful in detecting relationships, homologies, and common ancestry as well as in distinguishing species, populations, and other genetically different entities.

Wheeler continues:

"We are certainly justified in regarding ethological characters as very important, as belonging to the organism and as being at least complementary to the morphological characters. If this is true, our existing taxonomy and phylogeny is deplorably defective and onesided. To classify organisms or to seek to determine their phylogenetic affinities on purely structural ground can only lead, as it has led in the past, to the trivialities of the species monger and synonym peddler. . . . The fact that the morphologist has so consistently either neglected or opposed the use of ethological characters in classification shows very clearly that in his heart of hearts he has never very earnestly concerned himself with the parallelism of structure and function. He is inclined to regard function, especially psychical function, as something utterly intangible and capricious. For does it not seem to make its appearance in the embryo or young after structure has developed, and to depart at death before the dissolution of visible structure? And are not our museums largely mausoleums of animal and plant structures which we can forever describe and redescribe, tabulate and retabulate, arrange and rearrange, without troubling ourselves in the least about anything so volatile as function?

"It is, indeed, not only conceivable, but very desirable, that a taxonomy should be developed in which the ethological will receive ample consideration, if they do not actually take precedence of the morphological characters. It is certainly quite as rational to classify organisms as much by what they do as by the number of their spines and joints, the color of their hairs and feathers, the course of their wing-nervures, etc. To regard our existing purely structural classifications as anything more

than the most provisional of makeshifts, is to ignore the fact that the vast majority of organisms are known only from a few dead exuviae."

If all that is any less pertinent today than when it was written in 1905, than I am unaware of the fact.

Wheeler is now telling us that we cannot have a "whole" taxonomy which does not include functional as well as structural characteristics. No one would disagree with him--not even the thousands of systematists who wouldn't be caught dead including behavioral characteristics as integral evidence for their classifications and their hypotheses.

These arguments have not changed in the last 62 years. But I am interested in why they can be as appropriate today as then--in why zoologists turned behavior over to the psychologists decades ago, and have never clearly succeeded in recovering it in spite of repeated efforts and even when faced for a long time with the fact that psychologists have not been answering the kind of questions zoologists need to have answered about behavior. I want to know why, within zoology, the systematists have tended to leave the paltry amount of behavioral understanding that has developed largely to the "experimental" zoologists.

In his book, "Adaptation and Natural Selection," George C. Williams (1966) suggested that the problems of understanding selection, behavior and adaptation are not going to be solved by the methods of systematists. I take issue with this statement in one regard. There is a lot of narrow-minded systematic work which will not solve such problems. On the other hand, I really doubt that these problems are going to be solved until the systematists get heavily involved in them.

Now what's a systematist? I think a systematist is anyone who carries out broadly comparative work that includes phylogenetic relationships as a significant variable, or anyone who takes as his specialization in biology a group of organisms rather than a set of problems such as the nerve impulse or muscle contraction of something similar.

I am reminded by this of the Wigglesworth Law and the Inverse Wigglesworth Law. V. B. Wigglesworth is reputed to have said that for every problem in biology there is a group of organisms most admirably suited for its study. The Inverse Wigglesworth Law which followed quickly must have been formulated by a systematist, for it says: For every group of organisms there is a set of problems, for the study of which that group is most admirably suited!

Wheeler seems to me to have been speaking of a related problem when he said:

"There are, of course, enormous difficulties in the way of constructing ethological classification, quite apart from the fact that our knowledge of behavior is even more fragmentary than that of structure, as anyone will realize who tried to write an ethological description of some common animal or group of animals. In morphology the elements of description can be treated as parts of an orderly and traditionally respected routine, but in ethology we still lack the necessary preliminary analysis of the more complex

instincts, and are therefore unable to construct uniform and mutually comparable descriptions. One great desideratum in ethology at the present time is a satisfactory and sufficiently elastic working classification of the instincts and reactions, like that of the organs and organ systems of the morphologist. Such a classification can be developed only by comprehensive, comparative study of behavior in a number of genera and families and not by any amount of intensive study of a few reactions in a few species."

Wheeler's remarks lead to three conclusions with which I agree:

1. Behavior is the most diverse aspect of the phenotype, and systematists are the biologists most emphatically concerned with diversity.

2. Behavior is the most directly selected aspect of the phenotype. Recently, a botanist put me on the spot by suddenly demanding an answer to the question: "Well, what is animal behavior anyhow?" I didn't want to show any hesitation in front of a botanist, so I just blurted the first thing that appeared in my mind, and it came out: "Behavior is what animals have interposed between natural selection and the other (morphological, physiological) aspects of their phenotypes."

I have thought a lot about that definition a good deal, and I don't think I want to change it.

3. Behavior is the aspect of the phenotype most indirectly and complexly related to the genotype.

It is in this third statement, I suspect, that we can find a most prominent reason for the reticence of systematists concerning the use of behavioral characteristics. They want to know that the variations they use have a genetic basis, and so they have believed the experimental biologists who have told them that they must know all about the development of a behavior pattern before it can be trusted. They know how much they can change their own behavior, and so they are suspicious of variations in animal behavior, and they find it easy to believe the psychologists that all behavior is "learned," one way or another, without going to the trouble of figuring out what this actually means.

This dichotomy, incidentally, between learned and unlearned behavior, is in my opinion one of the most troublesome things in the study of animal behavior. It never has disappeared, from the time of the Greeks. Instinct and learning, innate and acquired, learned and unlearned--and the last attempt to make it respectable by cloaking it in new terms is in a recent textbook of animal behavior where it is called "endogenous and exogenous." I am going to say more about this later if I have time.

A few weeks ago I sat on a committee in which a group of behaviorists reported a list of problems in animal behavior that they thought are important today. I put down this set of problems so that I could read it, to give an idea of what the behaviorists think is important about their field:

1. Ontogeny of behavior

2. Behavioral genetics

3. Neural bases of sensory coding and coordinated movements

4. Biological rhythms

5. Behavioral neuro-edocrinology

6. Physiological bases of motivation

7. Emotionality and stress

8. Alertness, attention, sleep, wakefulness, etc.

9. Learning, conditioning, memory.

10. Higher neural functions.

11. Biology of mental deficiency, mental disease, and behavioral aberrations

12. Spatial orientation of animals, taxes, migrations, homing behavior

13. Ecological and evolutionary relations

14. The problem of the relationship between human and animal behavior

Of these items, the second and the thirteenth, I think are of most interest to us. Ultimately, all of them must be of interest to systematists, for, as I have stressed, systematics cannot ignore any kind of data in biology.

The ecological and evolutionary aspects of behavior are of most direct interest to systematists, and this group of behaviorists broke this topic down further into: the role of behavior in differentiation of the species and in isolating mechanisms; the comparative anatomy of behavior ("Not an active area but needs doing"); the ethogram as an important part of the data on comparative relations ("The natural history of behavior is in the same state that comparative anatomy was in 150 years ago"); changes in the gene pool as a result of selection; population density and behavior; habitat selection; migration; social organization; and some others.

Pause for Questions

Question: Hasn't some of the technology of the last fifty years been extremely important in the study of animal behavior--for example, the equipment that makes it possible to analyze crichet chirps?

RDA: Yes, and that's a good point to bring up. Sound recording and analyzing equipment, for example, is only about 20 years old. A man now at The University of Florida, James E. Lloyd, has just figured out how to translate firefly flashes into sounds and then tape-record them for later analysis. He is using the sound-analyzing technologies, in other words, to solve the problem of analyzing firefly flashes. The people working with chemical communication are still somewhat behind, but are beginning to use gas

chromatography. Many of the techniques and equipment used by behaviorists are very new and very important. But just plain watching has not gone out of style, either.

Question: I realize that your purpose is to emphasize behavior, but isn't it true that use of behavioral characters by systematists involves the same problems that are involved with morphological characters? That is, one still has to deal with such things as convergence, and even worse, . . .

RDA: Yes, that's true, but, after all, that is the way evolution works . . .

Question: Yes, I understand, but unfortunately behavior is frequently very plastic. People working with arthropods don't have the same kind of problems that people working with vertebrates have, but . . .

RDA: Well, let me ask a question to that: Do you know of any species differences in behavior in any organism that you have some reason to suspect, or that anyone at all seems to have a reason to suspect, do not have a genetic basis?

Question: I don't suppose there is any aspect of any animal that doesn't have a genetic basis.

RDA: No, I said any difference that does not have a genetic basis. Let me give an example of what I mean. In 1961, in the symposium on vertebrate speciation held at The University of Texas, Lester Aronson and Ernst Mayr got into an argument concerning use of the word "innate"--or one of the words in that general category--in discussing behavior. Mayr finally said something like this: "When you have taught one species of spider to spin the web of another species, then I will give up using the word 'innate!'" I think this remark has some significance in connection with my question to you. A while ago a behaviorist remarked to me that studies on the genetic background of behavioral differences among species are largely trivial and useless efforts. When they involve rather nebulous things like whether an animal requires, on the average, say, 30 trials or 40 trials to learn a maze, then I would agree. But there are many areas of investigation in the realm of "transmission" genetics involving behavioral differences, particularly between species, that are by no means trivial, for they involve some of the best clues concerning the extent and nature of developmental influences on behavior, hence, the nature of selective action on behavioral development.

[Note added in proof: Recently, Jerry Hirsch (In Spuhler, 1967) has pointed out that if all the data concerning differences in intelligence between variously related humans are assembled, they make up a picture that looks just as it should if differences in intelligence were strictly genetic in their basis. He goes on to point out that our efforts to improve the educational environments of humans across the world mean that in the future observed differences in intelligence are going to be increasingly owing to genetic differences and less and less owing to environmental differences. I can't think of an example that would illustrate my point here any better.]

Just after I first brought up this question I happened to think of a species difference in behavior which may possibly have no genetic basis. The spring and fall field crickets, Gryllus veletis and G. pennsylvanicus, usually have sparse and dense populations, respectively. Density of population affects aggression: crickets reared in dense populations are non-aggressive, those in sparse populations become highly aggressive. One observes differences of the predicted sort between field-collected individuals of these two species, but the differences can be erased by reversing the densities in laboratory populations. Thus, it is at least possible that the consistent difference in aggressiveness between field-collected individuals of these two species may not be related to any genetic difference at all.

Question: Well, since you brought up spiders as an example, I will use them too. When one tries to solve a problem in systematics, of course he uses every characteristic he can locate. Behavior has been useful in spiders, at the species level and at all levels, but it also gives some trouble. For example, there are two groups of spiders which build orb webs, and anyone just looking at the webs would think that these are the same types of spiders. But a look at the morphology of these two groups reveals rather basic differences. And after synthesizing the two kinds of information one comes to the conclusion that these are two different evolutionary lines. An orb web is just the most efficient way of catching prey, and these two lines have converged, now having almost identical web forms.

RDA: And if you looked back at the webs a little more closely, you would probably find something about the differences between them that would tell you that they are independently evolved.

Question: Yes, I'm sure of that--for example, you might find that there is a basic difference in the protein structure of the silk. But what I wanted to say is that it is really the synthetic approach that yields the most appropriate answers.

RDA: I certainly agree. That's why my phylogeny, if I may call it that (which I showed you on a slide a while ago), for the field crickets of eastern North America included life histories, songs, morphology, behavior, habitat, and other things. You remind me of something that happened as a result of one of the first papers I published, titled "The taxonomy of the field crickets of the eastern United States." Many people who read it said I should have titled it the taxonomy and biology of the field crickets because it contained much information that was not taxonomic in nature. I was stubborn, and I believed that all the information used was indeed taxonomic and didn't need any other name (One result of that was that no one wanted the reprints!). But a curious opinion has been expressed regarding that paper, to the effect that I am "that guy who describes new species on the basis of song alone." In fact, I have never done that. In the particular paper I mention, one can find considerable information on morphology (in fact, a repeat of all those morphological features studied by all of the previous taxonomists dealing with this group) as well as on song, life history, ecology, geographic distributions, and even crossing experiments. Yet in 1961 an orthopteran taxonomist published a paper revising the genera of Gryllinae and when he came to those species I discussed he referred to them as "species or subspecies, whatever they may be"--or in words very

similar. At first I gave him credit for acknowledging the possiblility that they at least might be different species, then I realized that this man has described practically all of his species on the basis of one or a few pinned specimens, most often brought to him by someone else!

I have wondered often if the kind of attitude that I have been characterizing is not related just to the fact that behavior is used at all in the papers involved. This is something like drumming individuals out of systematics not because of what they don't do, taxonomically speaking, but because of what they do in other fields or areas. B. B. Fulton, Harry Allard, and William T. Davis used behavior--but they avoided using it in their more taxonomic work. Fulton and Allard contributed mightily to the systematics of the Orthoptera through their behavioral observations, yet they have on occasion been omitted entirely from the ranks of orthopteran taxonomists. I have suspected for a long time that Scudder used song differences to distinguish North American field crickets, for he had them nearly correct away back in the nineteenth century, although his morphological distinctions are impossible to use or understand. I wonder if he left song out of his species descriptions because of the "prevailing climate of opinion" among taxonomists about such things? His classification was swept completely under the rug and has been there for more than fifty years now. Sometimes I think we have with our museums and collections built a monster which has been a terrible deterrent to systematic advance. Too many taxonomists have wielded their collections as weapons against the budding systematist rather than encouragements. Too often we have forgotten that the job of systematics is to solve certain kinds of biological problems, and collections were developed solely as a means to that end and have no other biological significance.

Question: Relative to the title of your paper, there is of course a problem of recovering the information in published papers, and the title should reflect as much as possible of the contents of the paper.

RDA: Oh yes, I agree.

Speaking of recovering biological information brings up an important point concerning behavioral study. I think that many of the old-time natural historians who worked out the natural history of wasps and other insects one hundred or more years ago knew as much about their animals then as anyone knows now, or can know. This bothers me very much, for it is an indication that behavioral study is not as cumulative as many other branches of biology. How do we make the study of the biology of animals a cumulative science? How do we record the behavioral characteristics of organisms in such a way that an accumulation of knowledge can occur? One of the current investigators who is really doing great work in this regard is Howard Evans in his studies on the comparative ethology of wasps. He is probably as closely focused on the kinds of things that interest me in regard to the relationship between behavior and systematics as anyone in the world. I noticed that someone reviewed his last book and lamented the fact that there were not more experimental studies in it. I think this lament is symptomatic of an illness in modern biology--the tendency to argue that there is some qualitative distinction to be made in biology between data derived from descriptive and comparative work and data derived from experimental work. There is not. Data are data, and descriptions, comparisons, and experiments

are not different in kind.

Question: But we have had trouble with the anecdotal nature of many observations.

RDA: Yes, largely because of anthropomorphism.

I will give another example along the lines of comparative and descriptive biology before stopping for coffee, and for it I would like to use man. I gave this example at Ann Arbor and someone said he was surprised that I "emphasized" man so much. I don't wish to emphasize man, but use this merely as an example.

We know that man evolved from apes. As George Simpson says, we always want to say, well, not really from apes but from the cousin of apes or something like that. But, he says, if what we evolved from was walking around today it would be called an ape, so we should really stop pussy-footing around.

What we don't know about man's evolution is how he evolved from an ape. We don't know what the selective action was that caused man's brain suddenly to enlarge. What caused men with larger brains to outreproduce men with smaller brains? How did man's brain make its dramatic departure from the general kind of brain possessed by other apes across the relatively short period of a million years or so? What was the nature of the selective action? We don't know. How will we find out? You say, well, we will have to scrape around at fossils. But we don't have many fossils, and I don't think, relatively speaking, we'll ever find out very much from fossils. But I do think we will find out. And I think the way we'll find out will be by comparative study. I think, furthermore, that we would have discovered by the same kind of evidence, in the absence of a single bit of fossil evidence, that man did indeed evolve from apes. We would have discovered this by comparative study that would have gone on long enough that we would have figured out on the side how evolution proceeds--its mechanics. The knowledge of inheritance, selection, mutation, isolation, and other evolutionary forces, together with information from comparative study of men and other animals, would surely have led us to the firm conviction that man evolved from apes. [Note added in proof: Desmond Morris' new book "The Naked Ape" points up the kind of comparisons I mean--whether or not one thinks any of the particular interpretations he makes are most reasonable.]

I think we can use comparative study to find out much about the history of selective action during man's evolution. For example, there seem to be four possible kinds of intraspecific competition or four different levels of intensity at which selection can operate on alternative genetic elements:

1. Indirect "competition": differential reproduction without direct interaction, and no confrontation between competitors.

2. Partial or complete exclusion of competitors from the best (or only) sources of food, mates, and shelter through aggressiveness and territoriality.

3. Elimination of competitors or potential competitors by killing them.

4. Intraspecific predation: cannibalism, or the elimination of competitors with food being obtained without additional risk or energy expenditure.

Of these four kinds of intraspecific competition, the first would usually result in the slowest evolutionary change, the others, in order, in increasingly rapid change. I think it is important for us to ask, with regard to man's evolution: (1) which kinds of competition were involved, (2) which were most likely predominant, and (3) what were the sizes and compositions of the units among which each kind of competition operated? That is, which operated only among individuals and which among social groups, such as families, of different sizes and complexities?

When I say that I think we can use the comparative method to solve problems such as this, it raises in the minds of some people the question: What is the comparative method in biology, anyway? Not long ago, an anthropologist expressed a not uncommon opinion in a discussion when he said that he wasn't quite sure what this comparative method is all about, but he didn't see how it could be very accurate or very useful. Someone should have been there to point out to him that it represented essentially the only source of evidence available to Darwin!

There is nothing mysterious about the comparative method as I am referring to it. Yet I am convinced that many systematists and other biologists who use it all the time scarcely know what they are accomplishing with it, are not sufficiently prepared to explain and defend its problem-solving value, and in any case could not give a clear exposition of its usefulness to systematics or to biology in general.

When I was trying to think of a good example to use to illustrate the comparative method this summer, I remembered a little discussion that I had gone through with myself relative to the question of speciation. After Bob Bigelow and I published our hypothesis that the two sympatric sibling field cricket species, Gryllus veletis and G. pennsylvanicus, had speciated without geographic separation by a process of accidental seasonal separation of adults, we got involved in some great arguments about the likelihood of this possibility. Some of the people in those arguments obviously had a great reluctance to admit that speciation might be possible without geographic separation even before they heard the hypothesis explained. It occurred to me that, even though I firmly believe that the vast majority of speciation occurs through geographic separation, I never had sat down and listed the reasons for my having this belief. When I tried to do it, they came out as follows. Unless I miss my guess, many of you would also have been unable to come up with this list of reasons, which reveal that essentially all that we know about speciation comes from comparative study.

We rely in the study of speciation, almost entirely upon information derived from the comparative study of a vast number of fragments of the speciation process. A bit of this one, a bit of that one, and the whole taken collectively, give us a composite picture that we can construct into a process from which we can predict rather precisely what must happen in any given individual case.

The picture that we construct, of course, (in over-simplified form) is that speciation in bisexual organisms usually occurs when populations become geographically separated and undergo divergence through divergent selection and differential mutations until they are sufficiently different to make hybridization either impossible or sufficiently disadvantageous that amalgamation is impossible. The evidence from comparative study which gives us this picture, I believe, can be summarized in five statements, as follows:

1. Practically all species are geographically fragmented. Geographic fragmentation, in other words, happens on a wide scale, and is likely candidate to permit much speciation.

2. These geographic fragments, taken collectively, show every possible degree of divergence from scarcely measurable up to what seems to be complete speciation. Geographic isolation, in other words, does lead to divergence of apparently the right sort, and in a great many cases.

3. Most sibling pairs or groups of species have a particular kind of geographic relationship: they are either allopatric or have relatively narrowly overlapping geographic ranges. This suggests that they were geographically separated in the recent past.

4. Cognate species are sometimes more divergent in the area where they overlap, suggesting that the contact there has occurred following geographic separation.

5. Pairs and groups of species that are not related--say, a pair of bird species, a pair of insect species, and so forth--often overlap in the same regions, suggesting a common geographic barrier that caused all of them to speciate. Often the probable barrier can be postulated with considerable confidence.

I predict, and I have some personal experience upon which to base this prediction, that no alternative to this process of geographic speciation will be widely accepted among biologists unless and until it can be documented in the same fashion--that is, until comparative study can establish sufficient replications of the individual steps in the postulated process to indicate the likelihood that it has gone all the way in one or more cases. In a paper in press in the Quarterly Review of Biology, I have tried to present such evidence for speciation by accidental seasonal separation of adults, postulated by R. S. Bigelow and me to have occurred in certain crickets.

This means, in part, that I think it is time we stopped fooling around with more theories, and more elaborate theories, about how sympatric speciation might occur, or could occur. Such theories are by now almost a dime a dozen, and can even be dreamed up by beginning biology students. The real question, as Ernst Mayr has pointed out, is the likelihood of their occurrence, and that question can only be answered if we get out into the field and accumulate the kind of comparative information that alone will tell us whether any particular postulated process does occur, and to what extent.

I would make one additional point about speciation and the kind of evidence from comparative study that I have just described. Many investigators seem not to realize that the list of facts I gave also represents a set of "criteria"--criteria against which one may in fact test whether any particular case of speciation that he wishes to examine is likely to have occurred as a result of geographic isolation. To take the extreme example, if none of the five statements I have just given seems to apply to, or coincide in any way with, the status of some particular pair of species, then I suggest that the investigator not only has an excellent reason for taking a closer look, but that he also has no right to assume that speciation in that case occurred as a result of geographic isolation without taking a closer look.

Ernst Mayr has said, and I appreciate the implication, that speciation is the most important single event in evolution. I have just argued that essentially everything we know about speciation has been learned from the classical kind of comparative study. I have also suggested that information from broadscale, even though relatively shallow, comparisons not only can enable us to predict with high confidence concerning specific cases, but also can provide criteria by which to test the significance of specific information about individual cases. This, I believe, is one of the best kinds of documentation of the power and usefulness of the comparative method in biology.

The kinds of evidence I have just been describing, incidentally, are those whose significance and validity are denied by anti-evolutionists--on a much wider scale than most people realize, I am afraid--and, further, whose significance is often downgraded and misunderstood, not only by physical scientists, but by many experimental biologists as well. Yet we rely almost wholly upon information from such kinds of comparative study for a wide variety of our concepts in evolutionary biology. It behooves us to understand this method thoroughly, and to be able to use and defend it facilely.

Life Cycle Changes and Sympatric Speciation in Crickets

(this section taken from notes)

Bigelow (1958) and Alexander and Bigelow (1960) postulated that Gryllus veletis and G. pennsylvanicus may have originated when a tropical species developed both egg- and juvenile-overwintering populations along its northern border. Masaki (1961) described a juvenile-overwintering population in the southern part of the range of the otherwise egg-diapausing species, Scapsipedus aspersus, sympatric with the parental population but with the adults of the two populations seasonally separated. In the eastern United States there is a temporally isolated, fall-adult population in the southern part of the range of G. fultoni, a species which farther north overwinters only in the juvenile stage and is adult only in the spring. Fulton (1951) and Alexander (1957) described temporally isolated, spring-adult populations in the northern part of the range of G. firmus. None of these temporally isolated populations is geographically isolated from the rest of the species.

These four cases all imply a connection between the appearance of a new life cycle and the multiplication of species. In fact, the presence of sibling species with radically different life cycles, such as G. veletis and

G. pennsylvanicus, is enough to raise the question whether the life cycle change contributed to the speciation process or was merely incidental to it. This question is particularly interesting with crickets and their relatives (1) because both of the common temperate life cycles occur within species as well as between siblings, (2) because no genetic difference is necessary for essentially complete temporal isolation of the relatively short-lived adults, and (3) because no case is known of spatial isolates with the two different life cycles, either sibling species or conspecific populations.

The next question seems to be: to what extent is it necessary or reasonable to postulate that geographic isolation was in some way involved in the development of life cycle differences between closely related species or populations of the same species? Alexander and Bigelow (1960), referring to G. veletis and G. pennsylvanicus, maintain (p. 477): "It is doubtful that the possibility of allopatric speciation could ever be completely ruled out, but the evidence suggests that geographic isolation is both unlikely and unnecessary in this particular case." Mayr (1963a), on the other hand, believed (p. 477): "It would be altogether unlikely for a population to adapt itself simultaneously to two different breeding cycles. Where a species evolves two such cycles it does so in different, geographically segregated, populations . . ." [and] "It is rather probable that the difference in breeding cycle of [G.] pennsylvanicus and [G.] veletis was not yet complete, when they first met, after emerging from their geographic isolation. If so, competition eliminated any tendencies for spring breeding in pennsylvanicus and of fall breeding in veletis." Alexander (1963) discounted the likelihood of Mayr's interpretation, pointing out that certain species have in fact evolved two cycles in one locality, but Mayr (1963b) responded (p. 206): "To me, at least, it would be far simpler to have the ancestral species of the veletis-pennsylvanicus group split into at least two border populations, one let us say east and another one west of the Appalachians, furthermore, to assume that in one of these egg-overwintering was more advantageous, in the other one, juvenile-overwintering, and that with the post-Pleistocene improvement of the climate, the two populations could overlap and coexist, owing to their previously established seasonal separation." Mayr concluded by repeating his earlier conclusion that "in not a single case is the sympatric model superior to an explanation of the same natural phenomenon through geographic speciation."

Mayr's (1963a) postulate that seasonal separation was completed because of competition following establishment of sympatry brings up some points evidently requiring clarification. Two kinds of competition could be meant: (1) between adults at mid-season, particularly in connection with reproductive activities, and (2) between juveniles of the two populations, or between juveniles of one and adults of the other, particularly in connection with food. It is difficult to imagine how either of these kinds of competition could be eliminated by shifts in life cycle. First, adult and juvenile crickets (possible excepting very tiny juveniles) live in the same places and eat the same things. Competition of the second kind, therefore, probably still exists between veletis and pennsylvanicus, and seemingly could not be changed by any possible shift in their life cycle. Second, competition (or interference) between adults of the two species also could not easily be construed to shift the life cycle, though it might adjust slightly the timing of the adult periods. The cycle itself is evidently restricted by possible over-wintering stages; there are no known intermediate

overwintering stages between eggs and late juveniles and, therefore, no seasonally intermediate periods of adulthood. The only possible "intermediacy" is represented by late adults of veletis or early adults of pennsylvanicus, but veletis and pennsylvanicus currently have about the same adult periods as other univoltine crickets overwintering respectively as juveniles and eggs, and lacking seasonally different, sympatric siblings. No evidence exists, therefore, that competition between veletis and pennsylvanicus has materially affected their life cycles.

Because of the history of the discussion about the significance of seasonal isolation in speciation, and the general attitude among biologists toward the possibility of speciation without geographic separation, it seems useful to account for other disagreements between Mayr (1963a, 1963b) and Alexander and Bigelow (1960) and Alexander (1963).

Mayr (1963b) (1) says that it is not stated how the northern and southern populations of a species such as the ancestor of G. firmus might have been geographically separated so that a process of allochronic speciation could occur within the northern segment (which Alexander and Bigelow suggested it may illustrate in part for this particular case of veletis and pennsylvanicus), (2) believes that not one but a series of peripheral isolates would have been involved, (3) suggests that there may have been an east-west split between two such border populations (contrasting this with a north-south split), and (4) believes that one isolate became solely juvenile-overwintering and the other solely egg-overwintering, and that speciation occurred allopatrically between them.

Concerning the first point, geographically isolated populations of G. firmus in the inland sand hills of North Carolina were first described by Fulton (1952), and later discussed by Alexander (1957), who noted that they hybridized with coastel populations (unpubl. tests by Fulton) and had the same song. Additional inland populations in Alabama have been found since then, some of which contain individuals with different life cycles. The example of a north-south split is, therefore, already before us in the proper species group, the right geographic locations, and (at least today) the right climate.

Second, the number of successful peripheral isolates does not seem to be important in assessing the significance of seasonal isolation in causing speciation. In fact, the more isolates there are, the more likely it is that allochrony was involved in this case, and the less likely it is that allopatry was more than incidental to the speciation process. The reason for this assertion is the following: if a species tends to produce populations with two kinds of life cycles, as, for example, G. firmus does, then an increased number of isolates will mean it is less likely that none contains both life cycles. The almost universal success of breeding tests among related Gryllus species that overwinter in the same stage, and the absence today of song or ecological (habitat) differences between veletis and pennsylvanicus, indicate that any persistent, double-cycled, ancestral population would have contributed genes to both incipient species. Accordingly, the significant isolation would still have been temporal from the start, and whatever geographic isolation occurred would have been quite incidental. In other words, speciation would have occurred in the north even if every isolate had been doubled-cycled. Furthermore, unless the temporal

isolation were effective as an extrinsic separator (in fact, capable of causing speciation), double-cycled populations would tend to destroy the effects of prior geographic separation when they became sympatric with geographic isolates (incipient species) that had developed different, single cycles while living in different places. In other words, even if there were evidence that geographic isolates sometimes develop different cycles (and there is none), we are not free to consider the fact by itself until we can eliminate the likelihood that double-cycled populations will also persist.

Third, whether the split, or separation of double-cycled northern populations from southern non-cycled populations, is "east-west" or "north-south" does not matter as long as it took place somewhere in the northern part of the range of the species--or in the region where there are mild winters, as there are today in the sand hill region of North Carolina where an "east-west" split is known to have occurred in G. firmus. Mayr's postulate of an east-west split on either side of the Appalachians is not unreasonable, but it confuses the issue since the only important point is that the involved populations must be separated in some fashion from the continuously breeding populations farther south in Florida; otherwise the latter would provide a means of indirect gene exchange between sympatric northern spring- and fall-maturing populations. This required break has no relevance to the question of geographic isolation between the two northern populations, which need never be allopatric during their speciation; three species, not two, would result from the one geographic discontinuity. Likewise, the particular timing of the geographic break relative to the genetic divergence of the sympatric northern populations from one another is of no relevance.

Mayr's fourth point of concern--whether life cycle differences now existing between siblings arose during allopatry or during sympatry--is evidently the only critical one.

First we should check natural populations for evidence. The four cases I have already mentioned are pertinent: Gryllus firmus, G. fultoni, G. campestris, and Scapsipedus aspersus. In all four cases populations with the two kinds of life cycles coexist in the same regions, in the southern part of the range of the three more or less northern species and in the northern part of the range of G. firmus, the only southern species. Recourse to natural situations, therefore, does not support Mayr's argument, for in no cricket, and to my knowledge in no other arthropod, are there allopatric populations with seasonally staggered life cycles correlated with different overwintering stages.

This finding is no surprise. The kind of life cycle shift it would involve can occur in three possible ways: (1) a continuously breeding population moving north in two or more locations could develop one kind of life cycle in one place and another in the other place, (2) one or more populations already having a single life cycle could make a complete shift in one generation to the other cycle, or (3) one or more single-cycled populations could develop a double life cycle and then lose the original cycle through extinction (shift slowly from one cycle to the other).

No case is known of the first of these three possibilities, which has already been discussed. But we should note that if it is used to account

for the origin of species such as G. veletis and G. pennsylvanicus, two problems are introduced. First, if a third (southern) derived species is involved, such as G. firmus in this case, then the near-identity of veletis and pennsylvanicus in a variety of regards in which they differ from firmus, such as chirp rate and pulse rate in calling, number of file teeth on the tegmina, and general size and body form, must be accounted for by parallel evolution or divergence solely by firmus from the common ancestor. Second, we must wonder why, in species like firmus and fultoni, all populations with one of the two possible cycles are inevitably small, sympatric portions of a large population with the other cycle; likewise veletis has never been found without pennsylvanicus, though pennsylvanicus occurs without veletis in Nova Scotia.

The second possibility above, a sudden shift in one generation of an entire population from one life cycle to another, seems too far-fetched to consider seriously. Only slightly less likely is the third possibility that some individuals would shift cycles and those with the old cycle would subsequently disappear leaving only the new cycle. But if we must involve allopatry this seems to be the only possibility. Requiring allopatric development of life cycle differences when sympatric duality in life cycles is known is to require not only a more complex hypothesis than is necessary, but a more complex one that is suggested by the facts.

Suppose allopatry is not required. Can the pairs of seasonally different populations persisting today, completely sympatric with members of the larger (parent) population still possessing the other (original) cycle, fail to diverge, over-wintering as they do in different stages and being subjected to different temperature and photoperiod regimes during the various parts of their life cycle? I believe that selection strongly favors divergence between such populations from the start, particularly in regard to overwintering behavior and physiology. Even if some gene flow occurred at mid-season between sympatric, differently cycled populations, or because of repeated shifting back and forth between the two life cycles, divergence would surely continue if only because of the selective advantage in the acquisition of different kinds of special overwintering characteristics, owing to the difference in the life stage that repeatedly enters winter.

One question that might be raised, and perhaps was involved in Mayr's objections, concerns the problem of survival of newly off-cycle individuals in the face of competition from the established population. Lewis (1966), for example, raises this question in attempting to describe how chromosomal reorganization may result in speciation without geographic isolation. That this problem is probably not pertinent to allochronic speciation in crickets is indicated by the coexistence of seasonally different populations within species.

If no gene flow at all occurs between seasonally cycles populations, then speciation would occur almost exactly as if the separation were geographic. If gene flow persists, however, then divergent selective action (roughly equivalent to a combination of disruptive selection and partial extrinsic separation) will result in speciation only if overwintering differences in some way eventually become linked to incompatibility.

Here an unexplained phenomenon enters the picture, at least with regard to veletis and pennsylvanicus. Among some 40 attempts to hybridize different cricket species, of which about half have been really intensive efforts, four of the five complete failures known to me have involved northern crickets with different over-wintering (diapause) stages. No hybrids have even been produced between species with different diapause stages, even though three investigators in North America (Fulton, 1952; Bigelow, 1958, 1960; Alexander, 1957, and unpubl.) have tried several cases. This is almost the only generalization about incompatibility between Gryllus species that can be erected at this time. Both copulation and oviposition (less frequent in the interspecific matings) occurred in all crosses tried by me, but no eggs hatched. Since populations of crickets consistently entering winter in different stages ought to develop appropriate diapause rather quickly, any strong reduction of gene flow between populations with different over-wintering stages could, therefore, cause an irrevocable shift toward total inter-sterility. This kind of divergence seems appropriately described in crickets as a "short route" to speciation, for total sterility is actually rare among sibling species of most or all kinds of animals. But early inter-sterility is not a required part of the process of speciation by seasonal separation outlined here.

Both spring and fall adults of firmus have repeatedly produced hybrids in matings with pennsylvanicus, but neither has hybridized with veletis. This may be an indication of ancestral northern affinities in firmus, and along with the more northward extension and greater northern abundance of egg-overwintering populations of firmus suggests a close relationship with pennsylvanicus. Because of this information, the possibility cannot be eliminated that firmus is a derivative of a pennsylvanicus-like ancestor, rather than vice versa. This would mean that, considering present distribution and sterility barriers, spring-adult firmus may be independently derived. It could also mean that veletis and pennsylvanicus may have diverged by production of a double-cycled population in the southern part of the range of a northern species rather than vice versa. This question affects the relative probability of the two models for allochronic speciation in explaining the origin of veletis and pennsylvanicus, but it does not reduce the likelihood that seasonal separation rather than geographic separation was the cause of speciation.

In summary, it would seem difficult to prevent genetic divergence between persisting seasonally different populations, even if they were sympatric, even if some gene flow persisted, and even if hybrids were not adult at the wrong season and did not enter winter during other than the two winter-hardy stages. The eventual result of such divergence would be two species that overwintered in different stages and were adult at different seasons, but had essentially the same habitats and occupied, at least initially, the southern portion of the parental range in the case of a northern species and the northern portion of the parental range in the case of a southern species.

There does not seem to be any easy way to derive veletis and pennsylvanicus except by one of the two possible variations of this scheme, which Alexander and Bigelow (1960) termed "allochronic" speciation in reference to the central role of extrinsic temporal separation. "Allohoric" speciation is a more specific term referring directly to seasonal separation.

It seems impossible even to gain an inkling concerning how frequently allochronic speciation may have occurred in various kinds of insects until intensive systematic-biological work has been carried out on a large number of temperate insect groups by investigators who are at least aware of the possibilities and know how the process can work. Such studies obviously have not yet been accomplished, for the possibility had not been considered prior to presentation of this case and that of Ghent and Wallace (1958). For at least three reasons I believe a large number of additional cases may be discovered:

1. Multiple-year life cycles and univoltine life cycles with short-lived adults are widespread among temperate insects (Pickford, 1953; Brooks, 1958; Alexander and Moore, 1962). Both involve potential temporal isolation of adults. As Walker (1964) points out, there is less expectation of rapid divergence in the case of multiple-year life cycles; geographic isolation of populations emerging on different years is also more likely, and is known in various cicadas (Alexander and Moore, 1962).

2. Unexplained variations in overwintering stage are prevalent in all major groups of temperate insects, both within and between species as presently recognized. Except for species with many generations per year, or long-lived adults that reproduce during successive seasons or cause overlap of generations, when such variations are intraspecific they lead either to multiple-year life cycles or to seasonal separation of adults. As an example of the possibilities, Brooks (1958) presents evidence that populations of a grasshopper, Arphia conspersa Scudder, in Alberta, Canada, contain some individuals that mature in two years, overwintering first as eggs and then as juveniles and producing spring adults, and other individuals than mature in one year, overwintering only as eggs and producing fall adults. Walker (1964) described two populations of a coneheaded grasshopper, Neoconocephalus triops that overwinter, respectively, as eggs and sexually immature adults and are sexually active during different seasons.

3. Cryptic species are abundant in every well-studied insect group, and most insect groups (tens of thousands!) have not yet been well enough studied to detect them. Every life cycle change that occurred within a temperate region could have involved allochronic speciation, and every pair of sibling species with different adult seasons and overwintering stages may properly be suspected of having speciated allochronically.

Even geographic speciation can only be inferred in the vast majority of cases. As a consequence there will never be a successful argument against those who insist that no alternative is possible. It does not matter whether this insistence takes the form of a flat statement of simply the rejection of all alternative hypotheses through construction of a geographic one that is continually altered and defended as more likely in the face of any and all evidence to the contrary. Speciation by other than geographic isolation may justifiably be inferred whenever sibling species are not geographically related in the ways common to sibling species, and when they simultaneously exhibit a striking ecological difference (such as a host difference or a life history difference) that separates their adults and does not appear to have arisen through competition or other interaction between the species. Such facts are not only inconsistent with a geographic hypothesis, they may cause the necessity of accounting for a geographic difference to become an onerous

complication. If, under the above conditions, an alternative to geographic speciation exists that is reasonable in its totality, based on the characteristics of the organisms under consideration, and if intermediate steps in such a presumed alternative process are found in natural populations, geographic speciation may be an extremely unlikely possibility.

In view of the importance of explaining rates and distribution of speciation, I think it will be unfortunate if attention to extrinsic temporal isolation is delayed by lumping it with some of the more outlandish attempts to explain speciation without extrinsic isolation of any kind, or discouraged by pronouncements deriving from previous arguments over the old specter of "sympatric speciation" in the sense of no extrinsic isolation. On the other hand, even if field crickets were so peculiar that allochronic speciation turned out to be trivially infrequent, I think we would still want to understand it in this case.

Pause for Questions

Question: Have you any evidence to show whether behaviorally, either veletis or pennsylvanicus is more like firmus?

RDA: No. I would like to see if northern spring firmus are less likely to cross with fall pennsylvanicus than with fall firmus and, vice versa, fall firmus with pennsylvanicus more likely with spring firmus.

Question: Can you break the diapause so as to synchronize adults?

RDA: It is easy to synchronize them by manipulating temperatures.

Question: Can you rear them easily?

RDA: No, the cultures weaken and die out after a few generations.

Question: What do you mean by "hybridize?"

RDA: I mean, just the production of offspring. We get cross-mating between veletis and pennsylvanicus, and oviposition, but no offspring.

Question: Do the embryos develop at all?

RDA: I don't know. Bigelow has some information on that but I can't remember what it is.

Question: Does the song of one attract the other?

RDA: Yes, it should. They are identical.

Host Shifts and Sympatric Speciation

Now I would like to describe another possible case of "sympatric" speciation involving host shifts in host-specific insects. I suppose that if I ever publish this I will have to use a pseudonym or I will indeed be labelled as another "sympatric speciation nut!"

In the summer of 1966, I travelled through parts of western United States tape-recording, collecting, and studying the ecological and geographic distribution of crickets, katydids, and cicadas. My chief aim was to complete as satisfactorily as possible a survey of North American crickets. The western tree crickets had been treated recently by Walker (1962, 1963), using methods similar to mine, so I was not expecting new discoveries in the Oecanthinae. In western Nebraska, however, in the Wildcat Hills of Banner County, I tape-recorded and collected a tree cricket on Ponderosa Pine. Its dark green color and non-descript trill, together with its occurrence on a conifer, indicate that this cricket is related to two eastern species not known to occur within 2000 miles of the Wildcat Hills in Nebraska: Oecanthus pini Beutenmuller, taken from several species of pine and balsam fir and known from New England to Florida, west to Arkansas and north to Ohio; and O. laricis Walker, known only from tamarack (larch) in southeastern Michigan and hemlock in northwestern Ohio (Walker, 1963). Indeed, Ponderosa Pine is known east of the Rocky Mountains only in western Nebraska and eastern Wyoming, several hundred miles east of the rest of its range.

This discovery caused me to pay more attention to Ponderosa Pine as I continued west. Sure enough, in the western Rockies and the Sierras, I heard a non-descript trill from Ponderosa Pine. For several nights I simply tape-recorded the song and made casual searches for specimens. I expected that this cricket was the same one I had collected in Nebraska, and at the least had no doubt that it was distinct from all the other western tree crickets. This opinion was based partly on my knowledge of eastern crickets, specifically the failure of any species to live on both coniferous and deciduous trees, and the relative host-specificity of those living on conifers. I was not disturbed that its song was not distinct from other trills, such as those of O. quadripunctatus Beutenmuller and O. californicus Saussure, for simple trills of this sort differ only in pulse rate and often sound very much alike to the human ear, especially in mountains as regions where temperature variations are often considerable from one collecting spot to another. I cannot distinguish by ear the trills of O. laricis, O. pini, and O. quadripunctatus.

The geographic distribution of the "western pine tree cricket," as I was thinking of it, also reinforced my assumption of its distinctness, for it did not correlate with any other cricket in the area. I heard this cricket only in fairly large pine trees, usually well out of reach (as with eastern pine tree crickets), and only at certain altitudes, it seemed, within the altitudinal range of Ponderosa Pine on the western slopes of the Sierras. The other trilling tree crickets in this area included O. californicus, abundant across most western states on a wide variety of deciduous shrubs and scrubby trees, both above and below the altitude of the pine cricket and always in the low vegetation several feet beneath the tall pines containing the "mystery" species. Walker (1962) records O. californicus from oak, almond, chaparral, juniper, pinon pines, and "small spruce-like

conifers in a scrubby area in New Mexico." But at that time I had not carefully read his description of hosts.

Near Mariposa, California, I climbed a succession of Ponderosa Pines and spent most of one night collecting, finally one male, one female, and one juvenile. The male was the second seen, and he was taken from a pine branch extending from a clump of pines full of this cricket into the foliage of a group of Gambel's Oak trees containing no singing tree crickets. As is common in such close intertwining of deciduous and coniferous branches, I needed only to trace the limb carefully to find the male, surrounded by oak branches, but perched on the single pine limb near its tip. I caught him by means of a ten-foot extension on my net handle.

I was astonished upon seeing these pine tree crickets, for they looked exactly like O. californicus, yellow-brown and broad-winged, and did not at all resemble the eastern pine cricket which are all more slender and greenish.

At this point I was convinced that the "western pine cricket" was a sibling of O. californicus, and was immediately intrigued by the ecological and geographic relationships of the two. The pine cricket seemed confined to a region wholly inside the geographic range of the more abundant O. californicus. It was more host-specific, lived on conifers, and was almost restricted to tall trees rather than shrubs and scrubby trees. Across more than two weeks of work, encountering both crickets nightly, it did not occur to me that they might be other than two different species.

I returned to the laboratory and made the interesting discovery that the songs of the two "kinds" of crickets are identical. Having a virgin female of O. californicus taken from oak and a male taken from Ponderosa Pine, I put the two together and watched their behavior. The male courted the female upon contact and she copulated with him within a few minutes, and repeatedly. There was no indication of incompatibility of any sort.

I am sure that these crickets are not different species. But this only makes their ecological separation all the more intriguing. There is no doubt that cross-mating between them is restricted by their ecological relationship. I am convinced that any individual is most likely to remain on pine or some deciduous tree, but not to travel freely from one kind of host to another. This bimodality, partly because of the host species difference and partly because of the difference in height from the ground, largely separates the breeding adults of the two populations, perhaps almost entirely separates them.

When I had been considering them as distinct species, and trying to figure out how they might have separated, I had started drawing parallels with the eastern conifer-inhabiting crickets and their relatives. O. pini and O. laricis are most similar to O. quadripunctatus, a species with the same ecological and geographic relationship to O. pini and O. laricis as O. californicus has to the western pine cricket. Further, in the East, pine trees are the first trees to appear in quadripunctatus habitat and they grow in clumps that increase in size and eventually contain massive center trees with no low foliage and are bordered by smaller seedlings. I reasoned, in fact, that the ancestor of pini and laricis could have separated from

quadripunctatus in the same way that the pine relative of californicus diverged from californicus. It was difficult for me to see how this could have happened geographically, first because in all of these cases the host-specialized forms are well inside the geographic ranges of the host-generalized forms, and I didn't see how one could easily postulate the host shift in an allopatric form so as to leave no crickets on the general large array of non-coniferous hosts. Moreover, in view of what I had discovered to that point, an alternative, sympatric hypothesis seemed highly reasonable. If individuals of O. quadripunctatus or O. californicus occasionally got on low coniferous trees, stayed there successfully, and they and their progeny were inclined to remain on pine, then as the pines grew and lost their lower branches, ecological isolation from the parent species would be enhanced. If dispersing individuals favored pine, exchange between pines could occur. Life on conifers would cause divergent selection, evidently because of predation since O. pini and O. laricis are colored so precisely like pine and larch needles, respectively, and probably also in association with food, host-finding, and other characteristics. The great ecological separation of pine crickets and their close relatives is indicated by the confusingly similar songs of O. pini, O. laricis, and O. quadripunctatus, which may not even be distinctive to the crickets themselves (Walker, 1963).

Finding out that the western pine cricket is not a distinct species does not reduce the likelihood that sympatric speciation has occurred between tree crickets. By demonstrating that habitat bimodality can appear without allopatry, it instead increases the plausibility of sympatric speciation in these insects through a spatial-mosaic separation of adults by host preference.

Tree crickets eat both plant materials and other insects, particularly aphids. The next steps in understanding this situation of course, are to test individuals taken from each kind of host for host preference and mate preference, and if host preference exists to see how it is established, whether by genetic differences or effects of the host on juveniles. Hybridization tests may be useful, and geographic distribution of each form, including possible variations in range of hosts, need to be worked out. Some attention must also be paid to hints of peculiarities in host-specificity and morphological and song divergence of populations in other species such as with O. nigriconris F. Walker, (Walker, 1963). Additionally, I have found that near Provo, Utah, there is a "form" of O. quadripunctatus on sagebrush foliage yet interspersed with normally green individuals on grasses and weeks. The trills of the two forms are slightly different. Again, a host difference is associated with a divergence that occurs now, at least, well inside the geographic range of the more widely distributed, more abundant form.

These cases warrant further attention, specifically in regard to the question of whether or not speciation without geographic isolation is occurring. The possible process is a variant of that originally outlined by Thorpe (1930), involving infrequent shifts between specific host, with host preferences based on some kind of early experience, and breeding and oviposition of individuals restructed to the host on which they developed. The means of separating gene pools is thus clear; the geographic relationships of siblings are unusual; and intermediate steps in the postulated process occur within species in the same genus. Perhaps there is not enough evidence

to argue that sympatric speciation is more likely than allopatric speciation in any case of tree cricket siblings. But there is enough to indicate that it could happen, may have happened, and may be happening and that special attention to this question is warranted in this case.

Pause for Questions

Question: Do these things have a one-year life cycle, only?

RDA: Yes.

Question: How do you figure the relationships among these species?

RDA: Morphologically and by song; they have the same color pattern, the same size and shape, and the same songs.

Question: Is the color confused by the matching of host color?

RDA: No, we use only the pattern--for example, the patterns of black spots on the antennae. Species groups in the Oecanthinae have similar patterns of spots.

Again, the only way we can solve the problem of the origin of host-specific pine tree crickets is by comparing all of the related species that occur on different hosts, or are variously host-specific, and, for example, by finding out whether any species are fragmented reproductively by host differences. In other words, our only recourse is to comparative study.

Raven: I certainly agree that sympatric speciation is a reasonable possibility and I also agree that this is a good way to approach it, but I want to ask you a couple of questions about the examples. First, how could you ever tell whether two species with life cycle differences arose in one place or two different places?

RDA: That's a good question, and I've often thought about it. One of the questions I've asked myself as a result is whether I have any evidence in any of the animals with which I deal that it is better to overwinter in one stage in one place and in another stage in another place? I can't find any such evidence.

Raven: Maybe it's a paradaptation . . .

RDA: Well, one also has to ask the question why there are no cases in which a species has geographically separated populations that overwinter in different stages when there are several that do show two overwintering stages in the same place and only one in another place.

Raven: Doesn't firmus have that in part? Aren't there some populations that are only juvenile-overwintering and some that are only egg overwintering?

RDA: There are only some that are solely egg-overwintering--none that are solely juvenile-overwintering. What happens is that the juvenile-overwintering population disappears as one goes north--as does the veletis

population. I suppose that the ability of eggs to overwinter farther north than juveniles is one indication of what I'm looking for, when you come right down to it.

Raven: Well, it seems that allopatry and allochrony are equally likely, in this case, but it is interesting to distinguish the two.

RDA: They are not equally likely.

Raven: They seem so to me.

RDA: I wish I could figure out how to explain to you that they are not. You don't need geographic separation and there is not reason to introduce it here.

Raven: No, I don't say you need it; I just don't know how to exclude the possibility.

RDA: I can't exclude the possibility. That would be like proving that speciation occurred this way. You can't do that. Prove how any pair of species formed.

Raven: Yes. We have examples very comparable in the subgenus Diadrena where oligolectic species occur sympatrically and have differentiated. For instance, one is a spring-blooming plant and another one is an early summer-blooming plant closely related to it. These seem very parallel and equally likely to have diverged sympatrically. But I don't know how to prove it.

RDA: I don't know about that case, but one of the things that have been introduced here and has done nothing but add to the confusion is the question of species that are adult at different stages but overwinter in the same stage. For example, Orchelimum gladiator is adult in spring and early summer, overlapping only a little with it very close relative, O. vulgare, adult in late summer and fall. This could well be a result of interaction, with some kind of competition between the species causing gradual divergence having nothing to do with speciation itself and occurring only after allopatric speciation. This is an entirely different kind of situation.

Raven: But there could be some advantage to blooming at a different time, or in the case of your grasshoppers to being adult at different times if they were using the same food source. And in your second case, involving host specificity, you have to assume that something like that is happening for them to get from one plant to another. You have to assume disruptive selection.

RDA: With regard to veletis and pennsylvanicus, they could still be competing very much with regard to food, but the juveniles and adults--especially the late juveniles--eat about the same things. [Note added in proof: But in the case of host-specific species, it's not necessary to have disruptive selection except after the fact of accidental isolation by moving to different hosts and then staying there because of some kind of response to the host on which the animal grew up or has been feeding--independent of any advantage or disadvantage as such. Disruptive selection need not be involved until after this happens. If the populations are already

separated, then the selection causing their divergence would be no more "disruptive than that occurring between two populations that happened to get on different islands--except, in my opinion, it would be more likely to be intense and effective between two populations on different hosts or with different life cycles than between two populations on different islands.]

I went through all that material on speciation partly because I wanted to promote the comparative method and argue for the need for more comparison in the study of behavior, and partly because I like to talk about speciation.

Behavior and Reproductive Isolation

An approach similar to that used in the analysis of speciation, and one that concerns behavior and also has been of great usefulness to alpha taxonomy in a few groups, has involved the study of reproductive isolating mechanisms. Reproductive isolation is so clearly the best understood liaison between behavioral and systematic work that I will go to some trouble to express some opinions that do not seem to jibe with much of the published, and evidently influential, literature, and to describe some of the arguments that underlie these opinions.

Although reproductive isolation is a relatively young subject, it has been discussed so extensively that one would suppose our ideas concerning it to be fairly well crystallized. Unfortunately, this is not the case. Presently, I think all of the good analyses of the actual reproductive mechanisms between pairs of species, in animals at least, can probably be counted on the fingers of one's hands. I say this in full awareness that some authors have been telling us that the literature on reproductive isolation is massive--so massive as to be almost not reviewable. This is not true. There is indeed a great deal of published information on courtship and mating behavior, and this is what our guides have been telling us is information on reproductive isolating mechanisms. But most of this information cannot be applied easily to questions about reproductive isolation. This is one of the ways that the study of animal behavior is currently out of focus; this would not be so if systematists were more involved in it.

I feel the same way about descriptions of mating behavior and their usefulness for studies of reproductive isolation as I do regarding descriptions of behavior in general and their usefulness for the analysis and understanding of behavior in general. One cannot just describe, sort of *in vacuo*: he must know what he's doing--what he is seeing in terms of life functions--before his descriptions are likely to make much sense or have much significance.

A few years ago, Paul Ehrlich said something in front of me that I sort of resented at the time. He didn't say it to me, but I resented it because of what I thought about it. He said, "You would never catch me studying the courtship of an animal unless I knew exactly what I was going to do with the information when I got done with the study." Frankly, I sometimes think Paul doesn't apply the same criteria to the study of morphological characteristics, but I understand what he meant. I think that as a result of carelessness in this regard of putting behavior into the proper life or selective contexts, what we are going to have to do in regard to much of the material being published in the behavior journals now is to start all over again.

You cannot go out and simply describe what you see in the courtship and mating behavior of a species, independent of where it lives, where and when it mates, with whom it lives, and to whom it seems most closely re - lated, and expect to discover very much of significance to anyone interested in reproductive isolation.

To illustrate this point, I will use the example given us by the extensive and elegant work of Tinbergen (1953, 1960) on gull behavior. While Tinbergen has provided much fine information on displays associated with courtship and mating, and some questions and speculations about probable isolating mechanisms, I believe that he fails entirely to comment on possible species differences in eye ring color. Yet, as a result of extensive field study, Neal Smith (1966) has presented data to show that merely changing eye ring colors among species that are sympatric is enough to break up pairs that are already formed, or to cause pair bonds between individuals belonging to different species, which apparently does not otherwise happen in the area where he studied them. Smith and Tinbergen did not study exactly the same group of gull species. But I suggest that anyone wishing to account for reproductive isolation in Tinbergen's species would now want to examine eye ring differences; and so would anyone wishing to use reproductive isolation to explain species distinctiveness in the displays of Tinbergen's gulls.

Species-specificity can evolve in many contexts other than reproductive isolation. Some of the interspecific variations Tinbergen has described may once have been reproductive isolators, but are not any longer. Or they may be involved in one of the other two possible functions of what we call courtship behavior--either the selection of superior or more compatible mates within the species or the synchronization of behavioral and physiological events between the male and female in connection with parenthood. Both functions are more likely to be prominent in animals like gulls, which have long-term pair bonds, or strict monogamy in some cases, and complex parental behavior. Mere species-specificity does not in itself mean isolating mechanism.

The chief point I want to make is simply that a tremendously important species difference evidently had been overlooked because reproductive isolating mechanisms as such had never previously been investigated among gulls.

[Remainder of this section taken from RDA's notes]

Let me dwell a moment on the succession of questions Neal Smith asked about reproduction isolation among gulls, for I think this is a good model for any of us to use when we attempt to investigate specific cases. Here is the succession of questions he asked: (1) to what extent do the different species overlap geographically; (2) to what extent do they overlap ecologically; (3) to what extent do they overlap temporally (seasonally); (4) to what extent do they interact (behaviorally) where they do breed together; (5) what is the significance of any morphological differences among them; and (6) what is the significance of their genetic differences for hybridization and hybrids? Now, of course, this is just the old familiar list of possible isolating mechanisms; but it's the order that is important. Anyone who does not ask these questions more or less in this order will not know whether or not he is studying isolation mechanisms among his species, even if he does prove that, say, genitalic differences or gametic incompatibility

prevent or partially prevent hybridization when sexually responsive individuals are brought together. If the chance of mating has never occurred in the field, then such differences may arise without ever having the opportunity to function in reproductive isolation. Under such circumstances they are neither isolating mechanisms nor isolating differences. They are just differences.

Many authors behave as though they think that any differences they find between species that breed in the same general area at the same general time are functional isolating differences or, even, evolved "mechanisms." In conjunction with this line of reasoning, it has become popular in recent years to speak, often glibly in my opinion, of "chains of partially effective reproductive isolating mechanisms." This casual approach misses the important point that some differences between species may never have been involved in their inability to interbreed or merge, or even in their living together without reproductive interference or competition. To use an extreme example, this is like saying that genitalic differences are reproductive isolating mechanisms between the Blue Jay and the White Oak, which happen to be sympatric, synchronic species that do not interbreed with one another. To take less "far-out" but equally ridiculous examples, it is like saying that genitalic differences are reproductive isolating mechanisms between two species of Drosophila that have always mated in different habitats, or between two species of cicadas that have never emerged as adults on the same year, or between two species of mammals that have never attempted cross-copulation.

A paper by Clark, Aronson, and Gordon (1954) on mating behavior in xiphophorine fishes has been referred to as a classic example of the study of reproductive isolation. But these authors did not investigate the interactions of the species of concern in the field; if the species do not even interact sexually there, then Clark, Aronson, and Gordon, too, may have been studying differences, but not isolating differences, and not isolating mechanisms in the sense of evolved isolating differences selected in the context of reproductive isolation.

Much discussion has been published on the question why, if selection works as I have just outlined, so many species that have never lived together have perfectly good pre-mating isolating differences already developed. The argument has been presented, evidently with much effectiveness judging from published references to this topic, that differences in pre-mating behavior between species living together usually arise not in the context of reproductive isolation at all, but in other contexts, and that they function only incidentally in reproductive isolation.

I believe that this argument (which sometimes seems related to a belief that sterility usually occurs before establishment of secondary contact between populations destined to remain separate) ignores the likelihood that, as reproductive isolation in the sense of minimal wastage of time and energy causes a focus on a few specific aspects of pre-mating behavior (such as calls in crickets, frogs, and birds, or odor in moths, or vision in butterflies), shifts in these characteristics in the context of reproductive isolation will be going on continuously. The result is that a species may be changed in a way that incidentally results in isolation from more than just the species causing the selective effect. A large proportion of species

falling into this category must shift their most important pre-mating isolators a little almost every time any change occurs in the complement of species with which they live. Two unrelated species, after all, may have confusingly similar signals. I suspect, therefore, that many of what we might call "incidental" isolating differences are owing directly to selection for isolation between (1) one or both of the two involved species and (2) additional species with which one or both of them formerly lived. If this is true, we would expect to find that species in groups which have come to rely chiefly upon one or two kinds of isolating differences (such as calls), would be more likely to be different in those characteristics upon first meeting than would species in groups that rely upon several kinds of differences (such as, say, chemicals, vision, host specificity) in different sub-groups. On the other hand, if reproductive isolating differences ordinarily arise in other contexts, differences between these two kinds of groups would not be so obvious.

If all this is true, one should expect to find in acoustical insects and anurans:

(1) few cases of identical pair-forming signals among allopatric or allochronic species. I know of only five or six cases among the approximately 1000 known calling signals of insect species (Alexander, 1967).

(2) few cases of character displacement. I know of only two probable or possible cases among the same 1000 insect species (Alexander, 1967).

The next pertinent comparison, obviously, would be between groups like the calling insects or anurans, and other groups in which one particular kind of signal or behavioral unit is not universally involved in reproductive isolation. Unfortunately, the information needed to make such a comparison is not readily available.

The Comparative Method and Reproductive Isolation

I have been talking chiefly about experimental studies, and about detailed observations on individual cases. How is the comparative method used in studying reproductive isolation, and what are its special values? A most striking parallel can be drawn between the results of studies on the calls of anurans and various insects (specifically crickets, katydids, and cicadas), and, I might add, the work of H. S. Barber (1951) and James E. Lloyd (1966, other papers) on fireflies. I don't think there is a single finding on anurans that does not have a close parallel in these insect groups, and I don't believe that any results on anurans, or insects, conflict with any results on the other group. What I want to emphasize, though, is one specific point: There are now experimental demonstrations that call differences between sympatric, synchronic, closely related species are sufficient to enable the males and females both to distinguish their own conspecifics; at least one demonstration exists for anurans, and one for each major insect group in which calls are prominent in breeding behavior (Alexander, 1967). For a long time, however, there were no such demonstrations at all. Yet we knew even then, or I should say were highly confident, that the calls indeed do function in reproductive isolation, and we used them successfully and accurately as if they did. Our evidence, like that used in understanding speciation, was derived from broad-

scale comparisons. It can be summarized in the following group of statements which to some extent parallel those I gave earlier for speciation:

1. The calling (or pair-forming) signals of species that breed at the same times and in the same places are never the same, except in a few newly established situations. This fact, based on comparison of nearly 1000 insect species alone, including essentially all of the North American crickets, katydids, and cicadas, and many of the grasshoppers and fireflies there, suggests that, in these groups, no two species breeding together are exempt from selective action on reproductive isolating mechanisms until their calling pair-forming signals are specifically distinctive. This, I believe, is a critical bit of evidence, for it indicates that no one can effectively study reproductive isolation in any group without being specific about whether the species involved breed together, and for how long they have been doing so. I would point out that many studies on Drosophila mating behavior, even those supposedly dealing with reproductive isolation are either vague about geographic, ecological, seasonal, and daily overlaps in breeding, or they do not mention them at all. No wonder it sometimes seems easiest to behave as though the origin of reproductive isolating mechanisms only incidentally has anything to do with living together!

2. Calling signals of species that breed in different places, or at different times in the same places, are sometimes the same. This fact, based on six known cases in insects, four of geographic isolation and two of seasonal isolation (Alexander, 1967) makes the previous statement even more significant. This is interesting in itself. Why aren't there more cases?

Question: How many have been looked for?

RDA: Oh! How can I answer that question? My first thought is to say thousands! In the groups that Tom Walker, Tom Moore, and I have studied, we have certainly been looking for displacement in every instance in which we have recorded geographic variation in calls.

I will give you an example in which we expected to find it and did not. E. S. Thomas and I studied three meadow grasshoppers comprising the Orchelimum concinnum group, which provide an almost ideal model for the expectation of character displacement. They all have linear ranges, two forming semi-circular ranges and overlapping only at their ends in Michigan and Louisiana and the third extending between the circle formed by the linear ranges of the other two and also overlapping with both of them geographically, ecologically, and seasonally, yet the songs are no more different in the overlap zones than outside them. The songs, however, are quite different so perhaps the differences arose during sympatry in one place a long time ago, perhaps in Louisiana.

I think that in species like these, using acoustical signals, when there may be up to 50 such calling species in one area, any slight shift in the species complement may cause slight song adjustments. The species involved may not even be closely related if there are enough of them sympatric and synchronic. Perhaps this would cause much song divergence between cognate species during allopatry.

Let me go back to my list of statements.

3. Calling signals of closely related species that overlap narrowly are occasionally more different in the region of overlap than elsewhere, suggesting reinforcement of differences owing to competitive interaction. Two cases have been suggested in North American crickets (Alexander, 1967).

4. Calling signals represent the earliest unit in sexually significant encounters between males and females. From an a priori viewpoint, therefore, these signals are the most efficient possible part of the sexual encounter for the function of reproductive isolation.

5. Calling signals are more species-distinctive than any other aspect of the mating sequence, and there is a progressive loss of species-distinctiveness as one considers events that occur later and later in the mating sequence. This statement is based on our knowledge of call distinctiveness in several hundred (all known) insect species with pair-forming calls, plus a study of courtship, genitalic structure, and mating behavior in some ten subfamilies, 22 genera, and 50 species of crickets (Alexander and Otte, 1967).

Call differences are behavioral differences, and reproductive isolating mechanisms in established situations must be behavioral nearly all of the time, even if the behavior involved is associated with locating the habitat or host to which mating activity is restricted, or with being active only at certain times of the day, as in some fireflies. Behavioral differences, if available to selection, will always be more efficient isolators, in terms of wasted time and energy, because they operate before morphological or physiological, or late-operating behavioral differences will, I suggest, always be replaced by behavior as functional isolators as selection continues between species that remain sympatric and synchronic. This argument indicates that no one interested in reproductive isolation can avoid studying behavior, and I believe that no one interested in species and speciation can avoid studying reproductive isolation.

A writer using almost exactly the same title as mine today said last year that there is no argument that behavior should replace morphology as the main tool of alpha-taxonomy in distinguishing species. But it already has, for groups containing, collectively, somewhere between 25 and 50 thousand species (Anura, Ensifera, Caelifera, Auchenorrhyncha, Lampyridae) and in the case of acoustical and visual signals it has proved to be of enormous (I would say, unparalleled) value, not only in distinguishing species but also in locating and collecting specimens and in tracing geographic and ecological distributions and seasonal life histories. This approach is, of course, not applicable to all kinds of organisms, for reproductive isolating mechanisms of certain sorts may be very difficult to identify and measure. Further, this method does not help us with forms that have never lived together. But the advent of new techniques and instruments suggests that anyone serious about alpha-taxonomy in any group of organisms cannot really afford to assume that his organisms automatically fall into a category of being inaccessible taxonomically from this approach. After all, 15 years ago we couldn't study sounds objectively, and only five years ago there were no gadgets to record the subtleties of firefly flashes.

The Problem of Instinct

[This section from notes]

To this point I have said nothing about what has undoubtedly been the knottiest problem in the study of animal behavior, and the one responsible, I suppose, for deterring the advance of comparative study of behavior more than any other. We could call this the "problem of instinct," and most people would have a good idea what is meant. It would be more descriptive to term it the problem of the extent and nature of hereditary influences on behavioral variations, both between species and among the individuals of each species.

Adaptation is a result of selective action on alternative genetic phenomena. Therefore, it is a critical question for my topic which behavioral variations at least do correlate with genetic variations. Few people challenge the idea that species differences in frog and insect calls, or firefly flashes, or any other behavioral characteristics identified as reproductive isolating mechanisms in any kinds of animals, have genetic bases. Of course, we know from hybridization experiments now that insect and anuran cell differences do indeed have genetic bases, and in fact results from crossing experiments on crickets and frogs are probably cited more frequently in reviews concerning transmissibility of behavioral variations than any others from any other kinds of animals.

The systematist wants to know more about this. He wants to know he can be sure that he is not examining some behavioral difference that has nothing to do with hereditary differences. Some systematists and other biologists have gotten involved in long, bitter, and futile arguments about how much influence heredity has in contrast to how much influence environment has in determining the characteristics of particular behavior patterns.

Concerning this topic, we are pursued now by a whole string of admonishments: "To ask how much a given piece of behavior depends upon genetic factors and how much upon environmental factors is like asking how much of the area of a field depends upon its length and how much upon its width." "Nothing is inherited but the genotype and a little cytoplasm." "Heredity is particulate, but development is unitary." "Instead of speaking of this or that trait as genetic or environmental, the correct way is to ask yourself which differences in which characters, and to what extent, are due to environment on the one hand and to heredity on the other."

Konishi (1966) has recently written a paper which, I think, clarifies several of the issues that have been involved in this problem. He points out that one of our shortcomings has been that we have acted as though the formula is always true that, in behavior, stereotype = species-specificity = inheritance = central coordination = spontaneity = self-differentiation. These things are not strictly correlated, and, as with learning, what has been called "instinctive" behavior is therefore not really a unitary phenomenon, and it should not be treated as if it is.

But these issues are not all of great or immediate concern to the systematist or evolutionary biologist interested in behavior. What is of concern is predictability. And the likelihood is great that significant increases

in predictability can be attained sooner in many cases by insightful, properly directed, broad-scale (even superficial) comparisons than by detailed studies of development of specific patterns of behavior in individual animals or species. The comparative anatomists, as many ethologists have emphasized, have already shown us that this is true. It would seem that we systematists have allowed ourselves to be led into being somewhat overly concerned about precisely how individual patterns of behavior develop. As a comparison, we do not know a very great deal, even in 1967, about the development of morphology in a wide variety of animals, but we do know a very great deal about speciation, adaptation, and phylogenetic history--all of it learned directly, almost solely, from comparisons of those very features of anatomy for which we still do not understand development.

When we have carried out broad-scale comparative studies of behavior similar to those available in anatomy and begin to acquire the glimmers of understanding that will come from predictiveness based on such studies, then those investigators concerned chiefly with the developmental bases of phenotypic differences will indeed have something to think about and work with. Since the question then becomes how to know how much genetic variation is involved, a considerably sharper focus should be provided for the investigations of many biologists who are now skeptical that broad-scale comparisons can be made in the absence of extensive information on developmental pathways and stimuli for particular behavioral units.

I expect this remark will raise some eyebrows, but I suggest that behavioral variations which look at first glance as though they might be useful to systematists, particularly those working at and above the species level, may rarely lack correlation with specific genetic variations. For example, as I asked before, would anyone here like to describe a species difference in behavior--that he has some cause to suspect does not have a genetic basis? Further, and of great importance, the extent and nature of correlations between behavioral variations and genetic variations, or their absence, is to a large extent predictable.

One aspect of such predictability can be exemplified by cricket calls. A slight understanding of cricket biology reveals that in most temperate species, only the eggs pass the winter. The auditory organs are not functional until maturation or near maturation. With only this information we can predict confidently that selection (at least usually) favors insulation from influences by environmental sounds in the establishment of the pattern of the call. For there can be no appropriate sounds available to copy.

On the other hand, only a little knowledge of passerine bird biology allows the reverse prediction: that most young birds probably have evolved specific ways of being influenced by their parents' song patterns. There are at least two reasons: the overlap of the young and adults each generation, and an apparent premium on individuality in song pattern, promoted by having part of the pattern learned, and associated with parental behavior and tendencies toward monogamy. Critical periods of song learning and imprinting of following behavior in precocious birds, are both predictable on this same general bases. Even the indiscriminateness of suitable stimuli for imprinting of following behavior is predictable, for the situation is such that unsuitable stimuli are not likely to be available, and selection will therefore have no chance to focus on a restricted group of them.

Likewise, we would predict that different populations of birds within species should sometimes have song differences that lack genetic bases, as with human languages.

The psychologists who chastised ethologists for erecting dichotomies with regard to learned and unlearned behavior were right, for many ethologists had their dichotomy out of focus. But when this argument took the form of rejecting all implications of important dichotomies in the manner of development of behavior patterns, it became a source of confusion rather than clarification. An important dichotomy can be identified in the examples I have just given: the question whether selection favors the use of a given stimulus, say, sound, in the establishment of a pattern in the same modality as the stimulus, or whether it specifically favors insulation from all stimuli in that particular modality. This is a dichotomy in direction of selection, and it leads to extreme differences in certain relationships between genetic phenomena and behavioral characteristics. We identify it and discover its significance by studying adaptation and natural selection in relation to behavioral development.

I would suggest that consistent selective action on any kind of behavioral variation, regardless of its original basis, will usually result in the presence, ultimately, of genetic variation relating directly to the behavioral variation. This would mean that the more ancient a behavioral difference is, the more likely that it has some genetic basis. Let me emphasize that I do not mean to imply by this any special kind of selection simply that selection will work on both genetic and non-genetic variations, but evolution will occur only when genetically-based variations become available.

No broad-scale attempt has been made to study adaptation in behavioral terms by the kind of comparison and prediction method of Darwin that I have just been describing. Yet such attempts should be fruitful if what I have just argued is true, even in dealing with the behavior of man, the most "labile" of all organisms in the functioning of his phenotype.

To show what I mean, let me use a simple example cited by Williams (1966). He notes that the females of many kinds of animals are usually described as being more "coy" or discriminating or reluctant in copulation than the males (or one could turn it around and say that the males are more "aggressive" in courtship), and he notes that this is predictable because the female invests a greater proportion of her total reproductive potential in each copulation or fertilization than does the male. If this argument is correct, then, as Williams points out, the situation should be reversed in parental animals in which the male is solely responsible for the zygotes, or more involved in parental behavior. Such reversals have indeed been reported in pipefishes in the genus Syngnathus, in which the males carry the fertilized eggs (Fiedler, 1954) (though not in all such fish: Breder and Rosen, 1966; Straughan, 1960), and also in birds, such as some tinamous and phalaropes, in which the males incubate the eggs and protect the young (Bent, 1927; Tinbergen, 1935; Höhn, 1967).

Similarly, reversals in which of the two sexes behaves territorially, fights off intruding individuals, and courts more aggressively, have been reported in some species such as the Ornate Tinamou (Pearson and Pearson, 1955), the Red Phalarope, the Northern Phalarope, and Wilson's Phalarope (See

Tinbergen, 1935; Hӧhn, 1967; Bent, 1927). Polyandry is more likely to be prominent in such animals and strict polygyny ought to be rare, although polygamy (or promiscuity on the part of both sexes) and monogamy have both been reported (Lancaster, 1964; Hӧhn, 1967). Polygyny, on the other hand, is prominent among species in which the females carry most or all of the parental responsibility, and polyandry is almost non-existent. Some of the disagreements in the literature (e.g., see Hӧhn, 1967) may result from differences in sex ratios among demes studies by different investigators. In some cases, what happens when sex ratios are locally or temporarily uneven may be important in understanding how selection has operated.

The relationship between reproductive effort and proportion of reproductive potential involved in any circumstance or event can be extended to include not only the proportion of eggs or sperm used per copulation, but also the proportion of the breeding season used per clutch or pregnancy, and the total probable reproductive life involved in each season, as Don Tinkle demonstrated on this program. Such considerations of proportions must also include the likelihood of changes in reproductive possibility, such as improvements through learning about one's mate or about the food and predators in one's territory, and the likelihood of improvement in weather conditions. Williams (1966) and Lack (1966) have pointed out that this means that longer reproductive lives, and that clutch sizes will increase with age. We should expect that, especially in long-lived, monogamous animals with specialized parental behavior, selection will continually maximize the slope of a line depicting the increasing reproductive ability of individuals and pairs.

Hereditary, Developmental, and Neurophysiological Basis for Cricket Stridulations

Someone asked me about plasticity in behavior, so I'd like to describe what we know about the genetics, ontogeny, and neurophysiological background of cricket songs. I think it's one of the more complete stories of this kind for any sort of behavior in any animal.

Acoustic insects not only grow up with little or no chance to hear the calls of their own species, they are also surrounded by a multitude of other sounds that bear little or no resemblance to signals they must eventually produce. A high percentage of the individuals in such species probably hear only totally foreign or inappropriate noises, and their own signals, during most or all of their lives, particularly during that portion of their lives when their ability to make the right noises in the right situation is developing.

It is not surprising that, in general, the communicative signals of arthropods do not depend in any way for their structure on perception of the signals of other individuals, of either the previous or the same generation.

The next question one is inclined to ask is: To what extent is a signaling individual influenced by his own signals? Do arthropods improve with practice or repetition of signal-producing movements?

Several investigators have deafened old adult male crickets and noted that their ability to stridulate normally was not affected. Except for loss

of ability to alternate or synchronize with other individuals, the only effects hinted at have been tendencies to stridulate for either longer or shorter periods than nondeafened individuals, results which could be obtained if auditory feedback has a stimulative effect and if other noises picked up by the auditory organs are sometimes interruptive.

To my knowledge, no one has previously reported destroying an insect's auditory organs before they had become functional, thus before it could have heard any sound, and subsequntly obtaining a song pattern from it. I tried this experiment unsuccessfully for several years with the snowy tree cricket (Oecanthus fultoni) because its chirps are so complex, and delivered at such an unvarying interval, and because the well-known mass synchrony of males in colonies suggests that auditory stimulation and auditory feedback are important. In August 1965, I was finally successful in obtaining two sequences of chirps (208 and 272 chirps, respectively) from a male defeaned as a juvenile (by cutting off its forelegs) before chirping began outdoors, and one sequence (too far from the microphone to analyze) from another deafened while still soft after molting to adulthood. Chirps were recorded by using an automatic recording device in operation twenty-four hours a day for eight days. They were produced in sequences, at least as long and uninterrupted as those of normal males. Wingstroke rate, chirp length, and chirp interval were all normal, and chirp intervals following occasional short chirps were shorter, as in the singing of normal males. The chirps of the male in which individual pulses (wingstrokes) could be analyzed were abnormal in one unexpected regard: the stridulatory apparatus was in contact during both opening and closing strokes of the wings, rather than just the closing strokes. This defect did not disappear from this male's song during several hundred chirps. Intrachirp variation, however, are common in this species, the known ones including pulse groupings and pulse omissions or weak pulses; Walker (1957) found that females and males respond to pulseless electronic chirps if they are the right length and properly spaced. I doubt that the abnormality of this chirp would greatly reduce its communicative value to males or females and I further suspect that it was not owing to the male's deafness but to thoracic damage caused by handling.

The most we can say of a positive nature about developmental influences on communicative signals in arthropods is that, with a few minor and doubtful exceptions, not a single one has been discovered; no one has found any way, short of actual mutilation or gross physical deformity, to alter the communicative signals of any arthropod. Wherever the internal environment of the structures responsible for the ultimate patterns of these acoustic and visual signals may be, the variable inputs of the developing individual's external environment must be translated into an essentially constant, species-specific milieu before they reach it. In what ways has selection brought this about?

Fulton (1933) conducted perhaps the first experimental hybridization of two species with different songs, and his study is still the most careful and detailed analysis available. He hybridized two North American ground crickets, Nemobius allardi and N. tinnulus, sibling species that are adult at the same time and overlap both geographically and ecologically, the former an inhabitant of grassy areas, the latter a woodland species. Fulton was able to analyze the songs of F_1 and F_2 hybrids and F_1 backcrosses with both parental species.

Fulton's results are in most regards straightforward: pulses in the songs of F_1 hybrids were delivered at intermediate rates, those in the songs of backcross progeny were generally somewhat more like the parent used in the backcross when compared with one another. There are some puzzles, however. The pulses in both backcross hybrids seem too slow; two of them are slower than most recorded tinnulus, and all but one of both kinds of backcross hybrids have slower pulse rates than the F_1 hybrids. The F_2 hybrids also seem to have pulse rates that are a little too slow--nearly all slower than the songs of the F_1 hybrids.

Two possible sources of error in the analysis could explain this discrepancy. First, Fulton had no method of counting pulses except by ear and by using a vibrating clamp that he could set by ear to correspond with the speed of pulse delivery in the insects' songs. As he cautioned, his counts above six pulses per second are probably somewhat inaccurate, and many of the hybrid songs were evidently heard only at higher temperatures and therefore were more rapid and difficult to analyze.

The second possible source of error involves the relationship between courting and calling sounds of N. allardi and N. tinnulus. One of the courtship sounds of both species is simply a slowed version of the calling sound. The particular courtship sound in allardi is quite similar to the calling sound of tinnulus, so similar that the insects themselves are probably unable to distinguish them. Some of the crickets whose songs Fulton analyzed may have been courting, not calling: he could have no way of telling certainly under all circumstances, and the possibility is especially great when large numbers of crickets are caged together as they evidently were in this case. With intermediate hybrid songs involved, the possibility of confusion is even greater.

Bigelow also crossed females of G. assimilis (a chirping species) with males of G. rubens (a trilling species). The hybrid males chirped and had wingstroke rates intermediate between the two parents (90 to 105 per second for assimilis at 70° F, 60 per second for rubens at 80° F, 75 per second for hybrids at 75° F). Bigelow concluded that the genes responsible for causing a field cricket to chirp are probably located on the X chromosome (σ XO, φXX). Those responsible for wingstroke rate variations are obviously not located on the sex chromosomes, since there was segregation of variations in these two characteristics as well as a probable difference in the number of genes involved in the differences between pulse rates and those between chirping and trilling. There is a suggestion here that song characteristics which stem from pacemakers located in different parts of the central nervous system have been altered by replacing genes located on different chromosomes. Since the differences between a chirping and a trilling song is simply a very long wing-hold interval which becomes the chirp interval, an interesting relationship exists with the findings of Fulton (1933) with trilling Nemobius songs having a very long pulse interval.

In all species treated so far, wingstroke rate differences between species seem to depend on a number of genes, while differences in patterning of wingstrokes (chirp patterns) may depend on a different gene or genes located on another chromosome (Bigelow, 1960). It is within reason that discovery can be made of the number of genes involved in pulse rate differences between species and the quantitative effect of single gene replacements

on pulse rate. Such information, together with studies of variation within species, is needed to elucidate how overlapping genetic differences between incipient species become effective in selective divergence.

In a series of publications, Huber (1955-1956) has discussed his findings that certain of the sounds in a field cricket's repertoire, and also a more or less nonacoustic wing-whirring prominent in some Gryllus species (preflight behavior), can be produced by stimulating the cricket brain and that brain stimulation in different regions causes different kinds of sound or wing motion.

The parts of the brain Huber stimulated, the mushroom bodies, receive fibers from the antennal lobes, and, presumably, imput from the antennae. The stimulation points eliciting aggressive stridulation, although not easily separated geographically as a group from those eliciting first transition to courtship, are generally somewhat peripheral to the latter. Since those eliciting aggressive stridulation are associated with effects of violent antennal stimulation and the others with effects of mild antennal stimulation, it seems at least possible that variations in the sounds elicited reflected variations in the size of the region stimulated that are related to normal variations in the intensity (and perhaps duration) of antennal stimulation.

The precise portions of the patterns involved above depend for their nature upon postulated "pacemakers"--either single neurons or small groups of neurons--located in the mesothoracic ganglion (wingstroke rates), possibly the prothoracic ganglion (wing-hold or chirp intervals), and in courtship stridulation, possibly the cercal ganglion. The postulated prothoracic ganglion pacemaker, most interesting to us at this point, evidently fires continually at specific, temperature-dependent rates unless specifically inhibited. Only light-dark cycles, contact with other crickets, extreme temperatures, and disturbances are known to affect the calling cycles of males with spermatophores, and the effect in all three cases is evidently inhibitory. The only stimulative effects which might be suggested are (1) stridulation of other males--known to be stimulative (Alexander, 1961) and (2) the effect of the presence or absence of a spermatophore in the spermatophore pouch (Huber, 1955). But crickets call without acoustic stimuli, and undisturbed crickets with spermatophores do not call continuously; the latter effect is not specifically known to be stimulative rather than inhibitory.

Pause for questions

Question: How do the physical characteristics of the stridulating organs affect the sound?

RDA: They don't affect the pattern. They only affect dominant frequency (cps) and the intensity.

Question: Is there no variation in those respects?

RDA: Yes, there is both individual variation and variations between species. But you could probably play Yankee Doodle with a cricket's song and if you didn't change the rhythm or pattern you wouldn't change the cricket's response. The effect would be only to change the intensity. Crickets of

grossly different sizes (say, Nemobiinae and Gryllinae) have such different frequencies in their sounds, and such different tunings of their auditory organs, that they can evolve pattern independently because they are not likely ever to hear one another. I think there's a point to be made here concerning the use of reproductive isolating mechanisms to arrange higher categories. The point is that when something like an acoustical system becomes prevalent in many species, there will ultimately be a hierarchy of patterns. Some aspects of the pattern can be used to identify genera and subfamilies.

Discussion by Eisenberg

This is the first of these meetings that I have had the pleasure to attend. I didn't realize what was expected of the discussant. Apparently, today I'm supposed to make a few extensions and it'll have to all be off the cuff. I'm a mammalogist, but I find myself in almost complete agreement with the principles and approaches derived from insect studies by Dr. Alexander. I'd like to review what I consider to be his major points and then develop one or two of them. First of all, I think that it's truly well taken that behavior began to make significant advances in correlation with significant advances in technology. The point's been made that behavior patterns are ephemeral--that is, you can't put them in a box and expect them to stay there. But with the invention of the motion picture camera, the advances in photography, and the advances in recording acoustical phenomena, we are now able to put something in a cabinet and refer to it. And it has been possible to accumulate information that is readily accessible to other workers, which has, let us say, had a greater reliability than a verbal description. Perhaps one of the reasons that the study of behavior lagged as long as it did was inadequate use of language, or inability to use language to describe events that are so completely dynamic as behavior. In fact, in most of the behavioral literature written today you'll still encounter problems on the part of an author conveying exactly what he means when he describes pattern X or Y in whatever language he may be using.

I think the second contributing factor to the recent renaissance in behavior study has been the acceptance on the part of zoologists that behavioral patterns may be treated as morphological structures--that is to say that they have a history, an evolutionary history--that the modes of thinking which we have developed in the last three or four hundred years, refined in the last 100 years, with respect to morphological evolution could be whole-cloth transferred to the process of organizing the data of behavior phenomena. Thus, we can't underestimate the importance of the acceptance of "Evolutionary Theory" as part of our working hypotheses in attempting to classify and relate behavioral data to the understanding of the biology of the whole organism.

Whatever we may be--systematists or taxonomists--we want to explain change. Given the application of evolutionary theory to behavioral phenomena, then our problem is to explain change in behavior. And naturally we accomplish this in the tradition established in morphology by comparison. One of the things that came through here, I believe, or should have, in Dr. Alexander's talk, is the fact that as a behaviorist--or whatever he chooses to call himself--he is not limited to behavioral data. Rather, in trying to understand change and in trying to interpret the evolutionary history, of his group, he calls upon all kinds of data--data with respect to the habitat of the animal, morphology, physiology, etc. In the last few slides we went from a mention of a chromosome to a flash of the nervous system, and so forth. I think that, in conjunction with this, I should add that most of us who do work on behavior patterns have escaped from the syndrome of being detached from the living organism itself. We are, I would like to think, concretely involved with organisms. The thing has to be alive in order to behave, and it has to be in an environment that at least gives it the minimum to express its repertoire, and as a result you are, when you are studying behavior, perhaps more involved with the biology of the animal, than is the case if you are isolated

in, let us say, an unnatural environment for, not only yourself but the organism also, picking over its remains. And I can't stress this enough, that the more you push on with behavioral studies, the more you become involved at the same level as the organism is, and the more you are placed in a position where what inside powers you may have, can be brought forth or expressed. At least this is my feeling about it.

In his discussion, Alexander pointed out, in the terminal phases, that the number of species that have been discovered is increasing at a tremendous rate by the application of this sort of unified concrete involvement with the organism and utilization of all types of data, including behavioral data. This means, I think, information, and as we acquire more information, we are being required to redefine the concept of species, maybe not the philosophical concept, but the way it is applied in nature. Now, it is easy to see that a person involved as Dr. Alexander is, and uncovering differences by incorporating new criteria for the analysis of his material, has departed from a static condition. In other words, his approach in the incorporation of new information is leading to further and further subdivision and, in so doing, a better understanding of the diversity of life. Now, of those taxonomists or systematists that I have had a chance to know, some labor under the idea that they are in a hurry to get the job done. And that job is to put a name on everything. And pretty soon they are going to have it done, you see, and everything is going to be named. Dr. Alexander touched on this, but can you see what is happening here to that philosophy? There is a great deal of security, I suppose, or satisfaction to all of us, in tying something up, in saying "Well, here it is. We've got it." But the more kinds of data you develop, the more information you accumulate, the farther away you get from a permanent, static situation. Therefore, to those who are philosophically oriented toward a closed universe, where they've got everything nailed down, the notion of incorporation of new methods for understanding organisms is a bit of an anathema because it leads to opening the system up again, and things are not always as stable as they once were. I think that the trends now reflect a different outlook on the part of workers in that we're not looking for closed systems any more, and we are willing to accept a certain amount of uncertainty in our day-to-day existence, even with respect to whether we're ever going to get the job done of attaching a name to something. I don't think anything could illustrate this better than in my own field where in 1959 a major taxonomic work on North American mammals appeared. We have all the ranges mapped out and all those species tucked away and defined. It is useful, but it's only an approximation. And it will always be added to and expanded to some extent. The extent to which it is, of course, depends on the aims of the investigators and the "Climate of the Times." Whether it's life-long, good or bad, doesn't enter into it. It's just a fact of existence. But, through behavioral studies, and through an involvement with the organism in the environmental complex, so to speak, you open up a number of new questions with respect to what speciation is all about. Refer again to the examples given of sympatric speciation and how it possibly could occur in crickets. For example, a great deal of time and energy has been spent discussing how mammals speciate--geographic isolation, and so forth. But very little attention has been placed on what actually goes on in the field. And the more field studies you do, the more you are led to accept the fact that the organisms do not behave very much like the models that have been proposed to account for speciation. There is a very great tendency in most mammals to form inbred groups, or in the broad sense, "clones." Everybody knows this

to an extent, but the consequences of "clone" breeding can't be underestimated. No one has really tried to assess the effect of "clone" formation; to assess how long they persist; to assess the effect this might have over time. It's much more difficult with mammals, because the generation time is longer. With insects, of course, where the generation time is shorter, they'll undoubtedly come up with an answer that will be directly applicable to mammalian studies sooner than we will.

No one pays very much attention to the influence of early learning experience and how it dermines mating patterns in space with respect to habitats utilized. No one has paid very much attention in mammals to how it effects feeding behavior and the choice of foodstuffs. No one, for example, has really investigated food preferences in smaller carnivores as a function of the maternal-young association, yet truly it is of great importance.

Thus, all I wanted to mention here is that any remarks that Dr. Alexander may have had with respect to sympatric speciation and divergence with respect to his crickets, I know are not necessarily confined to arthropods but might as well be taken as possible mechanisms that are coming to light through a more integrated approach to mammalian studies as well.

I wouldn't like to engage in any discussions of theoretical points on plasticity and non-plasticity unless they come out of the course of discussion. I am essentially in agreement with almost everything that your speaker has said this morning to you. There are relative differences, of course, but to come down to absolute differences I would be very loath to do that. I think I'll throw it open to general discussion.

Discussion

RDA: Insects are sometimes flexible--or, I should say, individually variable in ways that reflect differences in developmental stimuli. A good example came to my mind as Dr. Eisenberg was speaking. I have sometimes been asked to identify crickets that were stored by certain wasps in their nests. I have found that when the first cricket is pulled from the pile making up a particular wasp's prey, I can usually name nearly all of the species that will have been caught by that wasp. The reason is that each individual wasp tends to hunt in certain kinds of places: bushes, weeds, or some such place--and the cricket species living there are predictable.

Question: Are there any insects known in which behavior tends to follow a different evolutionary path than other characters, say, genitalia? There are many possibilities for this sort of thing--not just behavior versus morphology, but larvae versus adults, different stages of polymorphic species such as coellenterates and parasites. The problem then is classifying groups of organisms with different evolving systems that aren't necessarily correlated. I've been struck by how fortunate you are that the behavior and the morphology in these crickets do correlate. What would you do if you found two systems?

RDA: I'm trying to figure out what that would be like. I'm inclined to believe that when people think that is the case they probably haven't looked closely enough.

This is not a case of evolution in different directions, but genitalic differences in crickets in general do not appear below the generic level. They are more or less alike for the members of each genus, and this is generally true in crickets. I don't know how they could be evolving in different directions from behavior.

Question: Well, it is certainly true in the examples of life stages I cited.

RDA: I know what you're talking about, but I don't see how it applies here.

Question: You've been dealing mostly with animals having a potent calling system, but it struck me when you began talking about the ones on pine that chemical attraction to the host plant might be more important. This gets them out of the general enviornment and concentrates them.

RDA: Yes, T. H. Hubbell, who works on camel crickets, used to say to me, "I certainly wish my camel crickets had songs!" And I have always said back to him, "They do; you just haven't figured out how to listen to them yet." All animals form pairs--the gonochoristic ones anyway. They get together somehow. What we have to do is figure out how. You can count on it that how they get together is going to be important to the systematist. Sometimes it will be difficult to study, sometimes easy. But, after all, the study of sounds is only 13 years old. Anyway, you don't have to tape-record sounds to use them in taxonomy. William T. Davis used cicada sounds to identify species, and he got nearly all of them right long ago. Scudder evidently used them in the 19th century for crickets, though no one knew it. Phil Rau used moth odors by seeing which males attracted which females. He didn't have to find out what the chemical was. Riley, in 1897, or so, had a marked male moth return some miles to the female's cage.

But there will be variations, and one must be aware of the possibilities. For example, cicada males form huge aggregation. You know, people have been saying about mosquito swarms that they don't have a mating function because when you look at a swarm all you see is males. It's the same with cicadas, but you're looking on the wrong day. You've got to be there the first days. The first days the females are there too, and after a day or two the number of receptive females is very low unless there is a period of bad weather. We spent years studying periodical cicadas in the field before finally discovering that pairs are formed within the swarms, initially by visual stimuli. This means that species-specificity is likely to occur in the courtship signals, since swarms usually contain two or three species.

Question: How great a variation in song or morphology can a female cricket tolerate? In mammal breeding populations, for example, there are great variations.

RDA: Tom Walker has done most of the experimental work on that. I suppose I should say it depends upon the characteristic involved. In, say, frequency of the song, there's probably much tolerance; in pulse rate (in most sounds) not much.

I think we ought to remember that there is no individual recognition among crickets as there is in mammals and birds--parental animals that are often monogamous. Bird songs, for example, are under different selection pressures, I would suspect--species distinctiveness and individuality. The variability is not accidental or incidental. When you have this kind of selection you end up with an entirely different kind of behavior in terms of ranges of variation.

Question: What kind of individual recognition takes place in insects?

RDA: I don't know of any insects in which individual recognition occurs. I suppose caste recognition in social insects would be something approaching this. There are some monogamous insects. . . .

Question: I have a hard time understanding the ability of the females to recognize their own males at different temperatures.

RDA: The problem is even more complicated than you may imagine, for within the places where a given cricket species may be chirping, the temperatures may vary as much as 15°F, which is enough to erase species differences. Tom Walker's experiments indicate that the female's response changes with temperature, too. Males have to respond to trills of other males too. Huber found that extremely aggressive females often move their wings in the same rhythm as the males, indicating neuromuscular apparatus common to both sexes. That makes the question of how they change together during evolution easier, too.

Question: You asked a question and then you didn't really answer it, whether reproductive isolating mechanisms arise when the two populations are allopatric. It seems to me that the initial differentiation between the populations could be post-zygotic. That is, when they do come together there is some interbreeding, but--and you get viable hybrids, etc.--then you would expect a period during which the prezygotic mechanisms would be selected for because they're much more efficient. To me, it would not be surprising not to find a great deal of character displacement because it's the initial thing which is post-zygotic that is hard to pick up and may be transitory. You are studying the pre-zygotic mechanisms--the things which evolve later.

RDA: Yes, but that is character displacement if they are evolving later. In other words, in those cases in which there is fairly recent sympatry we should find character displacement.

Question: Well--not really. Say you have two populations come together. There is hybrid inviability. You would agree then that some more efficient mechanism would be selected for.

RDA: Suppose they are mating and producing hybrids. The females that are doing that are going to be at a disadvantage compared to any that recognize their own males and only mate with them. That's where the character displacement comes in, for if they're overlapping the only place where this kind of selection can occur is where they overlap. It cannot occur where they don't overlap, so the populations should differ in the two places.

I think we ought to remember that there is no particular inconsistency
between viewing it that way and also viewing it as a social process. That was
another conversation. Bird humor. Two computers can share different selective
perceptions; I would suspect--[inaudible]--[inaudible]--two human interlocutors.
Yeah, it is not exclusive or incidental. Where we have this shared
activity, it is not exclusive of intimacy. Where we have intimacy
we expect of mutual.

Question: What kind of relationship exists between these?

Dan: I think some of my feeling is that [inaudible] computer.
I suppose there exists an ability between [inaudible] to accomplish something
that, there are some accomplishments.

Question: I have a hard time understanding the ability of the Soviet
to reconcile their own needs as different communities.

Dan: The problem is even more complicated than the one question, re-
visits the living memory of [inaudible] that is, visiting the computer
rules are only as good as it is. Notice is needed to give accurate information.
The writer's experiences indicate that the people I visit, changes with
temperature, for. There seem to respond to visits to other sites too. Some
found that extremely objectionable [inaudible] they have only always to be sure
checking on the sites, [inaudible] maintaining objective common to both sense.
that makes the question of how they choose [inaudible] during evaluating makes
for.

Question: You asked a question and then you didn't really answer it,
whether reminiscence, [inaudible] evaluations relax when the [inaudible] ar-
alignments. It seems to me that the [inaudible] relationship between the
relations could be overwhelm. The [inaudible] when they do some complex dis-
is more interesting, maintain and [inaudible] avoid, etc. [inaudible] is
about a period during which [inaudible] would be relaxed [inaudible]
because maybe more effective. So on, it would not be more [inaudible]
to find a group who [inaudible] [inaudible] [inaudible]. It's the initial help
where is more [inaudible] in some of the way [inaudible] [inaudible]. You
are playing the [inaudible] [inaudible] [inaudible] where [inaudible]

Dan: [inaudible] to [inaudible] [inaudible] if they [inaudible]
to other people, to those people to whom there is still [inaudible] as
social [inaudible] [inaudible].

Question: Well--one really. Say you have two populations [inaudible]
There is still [inaudible]. You mean [inaudible] that they [inaudible]
[inaudible] would be [inaudible].

Dan: Yeah--one [inaudible]. Say you have two populations [inaudible]
[inaudible] [inaudible] [inaudible] [inaudible] [inaudible]

This topic raises the whole interesting subject of the extent to which interspecific hybridization is possible. I looked up a considerable amount of information on this subject in connection with lecturing on behavior and evolution and found that most animals seem to be pretty much like crickets. Hybrids are not usually difficult to obtain between species in the same species groups. Blair's results with Bufo, for example, are almost identical to those obtained with crickets. I have begun to wonder if some hybridization, when species initially become sympatric, might not be the rule rather than the exception. If that happens, disruptive selection may be much more important in speciation than we usually think, I wonder sometimes if we don't have the wrong picture built up in our minds about how speciation takes place. And we might be misinterpreting a lot of cases of hybridization. I wish someone would write a comprehensive treatise on the subject of hybridization.

Discussion by Raven

I was considering not saying anything. As a botanist, of course, I feel somewhat like an outsider because we have certain views of how things are. And one gets the impression that in zoology--at least, looking at it from the outside--there is this hard core of cicada, singing Orthoptera, fireflies, anuran people who have very definite signals they can work with. It may be that similar things will be found in other groups of animals but I could use the same argument to say that patterns similar to those found in plants will be discovered in many cases. The thing that really got me started was Dr. Eisenberg's comments which I thought were extremely appropriate and helpful. I would agree with both him and Dr. Alexander that one of the important things is that taxonomy is continually changing as new information comes in. And why I think that's particularly important I'll come to. But the key phrase that Dr. Eisenberg used that I liked is that taxonomy very definitely changes with the climate of the times. For example, I find that 40 years ago, botanists were emphasizing, above all, degree of morphological difference. And they could recognize populations as two species even though they said in the same publication that these two species intergrade completely. And by the same token they could recognize two things as varieties even though there were no intermediates between them. And they could recognize things as varieties too, parenthetically, even though they knew them to segregate in Mendelian populations. Now, today, of course, in botany as in zoology, in building taxonomy we emphasize discontinuities in the pattern of variation and we tend to recognize things as species between which there are discontinuities, and not to recognize things as species--at least not in the same groups--between which there is intergradation.

What this suggests to me is that exactly the same treatment could have been written a long time ago; the same very appropriate observations could have been made; and all the information could have been 100% correct. It is the information that is important.

In these groups there are certain standards used in taxonomy, as we see very well today, and I'm not arguing for a minute that these standards aren't perfectly appropriate in classifying these groups. What I will argue is that they're perfectly appropriate because the workers on these groups agree to use these standards; when they construct taxonomies on this basis they give them back the same kind of information that they put in. If one wants to emphasize reproductive discontinuity and if one has a running measure of discontinuity, it is perfectly logical to take this very heavily into account in constructing taxonomies.

But it also seems true that the more we really know about a group of organisms the less important the taxonomy is. It really makes very little difference how a really well-known group like Drosophila melanogaster or man is classified because when you really get to know a lot about an organism, the amount of information is so vast that the taxonomy serves mainly as a handle for getting back to this huge amount of information. In a sense, museum cataloguing is most important for the poorly known groups because in those cases probably all we have is a little morphology and anatomy. In other words, what we're really doing, I would say, is accumulating systematic information and recording it in appropriate forms, and when we record a lot of it the actual taxonomic decision probably makes less and less difference,

precisely because we discover intermediate situations, intergrades, etc. I could draw this out but it tends to lead us away from our point. I'd like, though, to mention the biological species concept. If anything, my view is that the biological species concept is very definitely to be equated with the climate of our times. And I think I could illustrate that. Making statements like: "So-and-so was correct forty years ago in making these taxonomic divisions,"--bothers me because he is correct only because our view of how one should construct species now agrees with his. If his information was good, and if he was a good observer that's one thing; but his taxonomic decisions can only be judged in view of the way that we do taxonomy now. Now let me illustrate that by tracing very briefly the history of the biological species concept in plants. The biological species concept in plants, as most of you know, was set up by Clausen, Keck, and Hiesey considerably ahead of Ernst Mayr's book. It was set up because they worked on a few groups of plants and they found certain relationships between them. They hybridized them, and they said, "Wow! This is absolutely fantastic! Let's chuck out the whole rule book! If you want to know if something is a species, you cross it and it's intersterile. An if it's inter-fertile it's not a species, and that's it!" And, so it was. They wrote that down on paper; they specified operations you could follow for checking it, and that's the key point. And what happened? Lots of botanists got samples of populations from all over the place, hybridized them, and what did they find? They found a mess. Apparently, they found that these standards wouldn't work. They found that if the species in a group were separated by strong barriers, that the populations within that group would be inevitably separated by strong barriers. They found that many species of plants have no reproductive isolation whatever; perhaps they're allopatric or perhaps they are maintained for some other reason. They found, in short, that the rigorous biological species concept of Clausen, Keck, and Hiésey which was perfectly operational--perfectly operational--you knew exactly what you had to do--did not give you a whole series of equivalent units in plants that were useful or that you would really want to call species. Now what about this at the present-day stage. If you ask a botanist, "Do you believe in the biological species concept?", he says, "Yeah! Great! You know, the biologcal species concept." What that means to them is that plants are alive and have properties--biological properties. Franz Stafleu, whom some of you may know, came up to me after the Ann Arbor Conference and said to me, "Why I believe perfectly in the biological species concept." And I said, "Franz, do you believe that if you cross things and they're intersterile they're different species?" He said, "No, certainly not; that would be absurd." And I said, "Franz, if you cross things and they're inter-fertile, are they the same species?" He said, "No! Absolutely not." So when you get to that point, what is the biological species concept--other than that for which it's been extremely useful--namely, focusing the attention of taxonomists on biological phenomena.

Now, I'm not at all convinced--Ithink there may be many dedicated zoologists who have little reason to think that species in their groups are exactly like species in crickets, cicadas, anurans, or fireflies. And I'm not really convinced myself, from reading the literature on birds and mammals, that species in those groups really correspond very well. You read studies of genera such as Diplodomys and Peromyscus, and you read what people say about the units that they're calling species, and the decisions that they're making about whether to call them species or not--I think they're fine, but I find them pretty darned equivocal--you know, they say they mate or they don't mate,

or something. What is a biological species in Thomomys, for instance? Who knows? Here are all these units. You can classify them, but what does biological species mean there, in the sense in which it is used in studies of crickets. Can anyone tell me? I think it's fine for Ernst Mayr to say that things occur together and they don't intergrade, therefore, they're biological species, but what he usually means by that is that there are two specimens from one mountain range, and that's where they occur together, and they don't intergrade so they're biological species. Well, what does he know about the genetic flow within those species, or the degree of isolation within those species. There's apparently nothing known about phenomena of that sort in birds. It's very easy to talk about complete gene flow within and no gene flow between if you don't know anything. But where do you get that information? You get that information by going up to a big drawer full of specimens and you say, "Gee, all these things look the same. There must be great gene flow in this species."

RDA: I'm trying to figure out how to remember all these things. . .

Raven: Sibley, who is going to be here tomorrow--what did he find--the best taxonomic way to divide the two towhees in Mexico is to draw an arbitrary line, ten miles east of Morelia, Michoacán; that's the only practical way for separating two units which you obviously want to call species.

RDA: You're mixing up a complaint that taxonomists are sometimes narrow-minded, or make mistakes, or deal with incomplete information, with a complaint that evolution is complicated. And who the devil uses the biological concept to mean inter-sterility? I don't know anybody who does anymore--except maybe a few high school teachers.

Reproductive discontinuity does appear. Bluejays don't hybridize with oak trees--maybe we can start there and work from that point. Reproductive discontinuity appears; it is an important event in evolution. As a result, the identification of it is important. The fact that it may appear and then disappear--emphasize that, if you wish, for that is important, too. . .

Raven: But by setting up a unit like biological species which you think absolutely applies to all groups. . .

RDA: That's another point I want to argue about. Who said it applies to all groups? I never said it applies to all groups.

Raven: Well, if it doesn't apply to all groups, biological species is one heck of a term.

RDA: Well, now look: even if it doesn't apply to all species absolutely, we can still talk about it for these groups it does apply to. And as for those people who are working with organisms where it does not apply--gee whiz! Find out what happens! I might be interested in finding out about sympatric speciation, but I don't resent people talking about allopatric speciation because a couple of my animals might have speciated sympatrically.

Raven: I think it's a little different. There you're talking about kinds of processes. In the one case, the term biological species seems to be a system of classification which could be applied, at least in theory, to everything.

RDA: You know, I've been worried--I really think one of the most important get-togethers that can be had in systematics is between botanists and zoologists, although I don't think that you would argue that your arguments are typical of all botanists. Nevertheless, I think that this would be a really important get-together, because they seem to think that their organisms are so different.

A few days ago I was walking up a valley in the Appalachians and I saw again for the umpteenth time two plants growing next to one another that the botanists call poison ivy and poison oak and say that they interbreed and hybridize and merge and mix and everything else. I have never seen one of those hybrids yet, but I've seen a lot of poison ivy and poison oak.

Raven: You're confusing two things. You're confusing whether reproductive isolation is an important evolutionary factor or not--which obviously it is; it's responsible for these patterns--and whether you can talk about identical units.

(Some unintelligible argument and laughter)

Question [to RDA]: Poison ivy and poison oak are not sympatric in the Appalachians. I don't know who told you that, but. . .

RDA: Nobody told me that. I will check into that because I'm really interested--wow! Are you sure? [Note added in proof: He was right: Poison oak is a coastal plain and sandy area species and the overlap between the species is entirely east of the Appalachians. But I was actually east of the Appalachians in Virginia during the above observation, and I think this is the only error in my story: the two species are now considered distinct, and no hybrids are known, in spite of considerable geographic overlap and a long history of opinion that they were not distinct].

I wanted to ask if you have used the biological species concept as a standard of comparison in order to arrive at the conclusions you just expressed.

Raven: Not at all, because I think it confuses the very important evolutionary facts of reproductive isolation which are about as diverse as the situations that occur. And, if I think there are some units I have to slam everything into, I lose information, I don't gain it.

RDA: But why do you think this is a unit that everybody can slam everything into?

Raven: Well, if you can't, what is it?

RDA: It is like mammals: All animals aren't mammals but we don't tell the mammalogists they can't talk about mammals.

Raven: I'd say in regard to populations that I don't know beforehand what kind of units I'm going to find.

RDA: That's fine. . .

Lunch

Afternoon Discussion

(unintelligible)

RDA: Yes, I think phylogeny is a very important aspect of systematic and evolutionary studies. I would say that speciation, mechanics, and phylogeny are the three general problem areas in evolution. Sometimes, one gets interested in phylogeny almost necessarily as a result of other studies. For example, when I first started to study mating behavior in crickets, I got interested in why they copulate as they do, and in attempting to account for this in a broad comparative study, I ended up discovering that all of the winged insects copulate, but all of the primitively wingless insects transfer sperm indirectly. I don't know what that means, but I find it very interesting. One of the most interesting problems is accounting for the indirect copulation of the dragonflies, in which the male transfers the sperm to a specialized location near the base of his abdomen before transferring them to the female. Neither the morphologists, who called this transfer apparatus, "secondary" genitalia, nor the behaviorists, who have concocted fantastic schemes to account for the evolution of this peculiar behavior, supposed that its precursor was indirect spermatophore transfer, say, via the substrate or through use of the male's legs, as surely was the case.

Question: I am curious about your remark that genitalic differences don't occur except at around the generic level in crickets, when in many insects such as beetles there are striking species--specific differences--often distinctiveness at subspecific levels.

RDA: Well, every group is different. I have a graduate student working on grasshoppers, and their genitalia are very complex. I don't know how one explains this, in itself, but it is probably partly responsible for their being more likely to be species-distinctive. He finds that in some of these grasshoppers, the first thing that happens in a sexual encounter is that the male leaps on the female--in fact, he may leap on any moving object about the right size. In some cases of mistakes, he leaps right off again; in others he does not leap right off but is repelled by the mounted individual. In some cases, genitalic differences may actually be analogous to, say, song or courtship differences, in terms of their place in the mating sequence and their role in reproductive isolation.

There are many reasons for changes in genitalia. We have found, for example, that when a cricket species becomes subterranean, evidently there is always a change to end-to-end mating from the usual female-above position, and this means that certain changes in the genitalia can be predicted.

But I wouldn't want to predict why your animals have species-specific genitalia. Are you sure each genitalic type is just a single species?

Question: You can tell the species better on genitalia than any other way.

RDA: What group is this?

Question: Water beetles.

RDA: One of the things it seems to me you should want to know is whether these genitalic differences prevent interspecific copulation.

Question: In this group I don't know.

[Much discussion unintelligible]

(Discussion on biological species concept: First portions unintelligible)

Raven: I don't know what to predict about the kinds of evolutionary units I would find until I studied [the populations].

RDA: No, but just knowing there are certain kinds of species in other organisms wouldn't so prejudice you that you can't study them would it?

Raven: It would blind me.

RDA: Would it? Really? I don't think it would. With these crickets I was discussing this morning, I was describing some really tough situations that don't fit with the usual picture. I don't know what it means to find populations with slightly different songs on different hosts. But I think I understand the significance of it better because I have a background in what the other populations do. This is what makes me realize how important it is to figure out this situation.

[Unintelligible discussion]

RDA: Well, I'm serious [about the problem of how taxonomic and other biological information grows together]. I am reminded of these guys who say they're going to do a slambang job of studying, say, the Drosophila of Hawaii or the grasshoppers of Australia, or something--and they're going to hire a taxonomist. Now, I don't understand what that means, and I think it's a deplorable situation. You hire a taxonomist and he writes up the taxonomy, and you take his taxonomy and work it together with whatever you're doing. But you always use his taxonomy. Well, fiddle! The morphology of the chromosones is taxonomic information--and so is everything else. Taxonomy is not something you do, and then you have it, and then you do the biology.

[Unintelligible discussion]

Well, you can't just study every characteristic of every organism. You must select those things most likely to be important.

It seems to me that pre-mating behavior is going to be of more interest in the future because of these demonstrations of their value in analyzing populations and their relationships. Obviously, not all animals have chirps, but bisexual animals will have some kind of pre-mating behavior.

If you have a prejudice or a bias, the thing to do is try to discover its basis. Only in this way can you discover whether it is justifiable or not--or make it useful rather than a liability. Objectivity comes from working with the greatest background of information, not from a vacuum.

[Another 45 minutes of unintelligible discussion]

MOLECULAR SYSTEMATICS

Charles G. Sibley

Yale Peabody Museum

When I speak of "molecular systematics," I don't mean chemistry; I mean morphology, i.e. structure. The moyphology of molecules is just as pertinent to a comparative approach as any other aspect of structure.

This is a strictly Darwinian-Mendelian approach, and comparison is the basis of it. I believe that we can obtain an index to genetic relatedness by comparing the structures of homologous proteins. Genetic relatedness is the term that I think is useful here. I don't like to use the word "phylogeny" because this is a separate problem. It becomes a separate problem because it doesn't matter how long it took to get how different; what matters is how different two organisms have become.

The goal of molecular systematics is to make precise measurements of the genetic distances between organisms, and to express these distances numerically. The numbers would be the number of nucleotides that the two organisms hold in common. This isn't a matter of inventing a number; it is a matter of discovering it, and I submit that such numbers exist. The goal, then, is one of precise measurement rather than simply the comparison of characters of unknown information content, which provide us at best with the basis for an opinion, but never with incontrovertible proof. If we can make these measurements then there can only be one answer, so our goal may be said to be to take the taxonomist out of taxonomy, and to substitute precise measurements that need only be made once for a given genetic distance. Now, can we really get such answers and such numbers?

Let us turn to a consideration of what protein structure is, where it comes from, and what it can do for systematics. The recipe of how to build an organism and all of the things it is going to do which depend upon a genetic basis are encoded in the structure of the genetic material, DNA. This structure is essentially a message, a description of the entire organism and what it does. The DNA simply encodes the information units in a linear sequence. The DNA message describes how to make the organism and how to make it work, and I would suggest that it even predicts most of what it will do, its ecology and its behavior.

Decoding the linear sequence of nucleotides of DNA is a difficult proposition. After you have done it with one organism, it still isn't feasible for use in systematics. One day we may find ways of identifying the homologous segments quickly. We can do it now using "hybridization" techniques, but these are not feasible for widespread use in systematics.

A triplet of nucleotides is a coding unit of which there are 64 possible combinations, designating the coding triplets at the level of DNA, and each one at the DNA level specifies the complementary triplet at the level of messenger RNA. The RNA messenger becomes associated with one or more ribosomes and protein synthesis is achieved by the assembly on this template of a series of amino acids which are specified for by the coding triplets at the level of DNA. The amino acids are assembled there by a second kind of RNA, transfer RNA, of which there are 20 kinds, one for each of the 20 kinds of amino acids. The amino acids are

assembled in a linear sequence, peptide bonds then form between them, and the resulting polypeptide chain which peels off the template is a reflection of the sequence of coding units which directed its synthesis. The remarkable thing about this process is its simplicity.

DNA then is a genetic material and the genetic code is universal as far as one can find out. All of the experiments to date have shown that all organisms use the same coding triplets, suggesting a monophyletic origin for life. Since the code is universal, it becomes meaningful to compare a plant with an animal, which would be meaningless at the level of gross morphology. We can also find their homologous proteins. Protein synthesis says to us that there is a genetic transfer of information which starts out as a sequential message and is coded in a four unit code which is translated into the twenty unit code of proteins. Sequence is the key to this whole problem.

A polypeptide chain by definition is the single chain of amino acids which results from synthesis from a single gene, and some proteins have more than one polypeptide chain. Hemoglobin, for example, is composed of four chains. A gene, by definition, is the sequence of nucleotides which determines the synthesis of one polypeptide chain.

Let us define one important point in relation to proteins and that is convergence. At the level of proteins, convergence must be defined as two sequences of amino acids which are now identical but which began in some ancestral form as different sequences. This is important because when we turn to electropheretic comparisons or other kinds which don't give us amino acid sequences, we must be careful not to talk about convergence when two patterns are similar.

What is the probability of convergence in protein sequences? It is essentially zero. A sequence of only seven amino acids can be arranged in over a billion ways. A sequence of a hundred or two hundred amino acids comes out to a number larger than all the ultimate particles in the universe. Most proteins are reactive chemical units. But, whereas a great part of the structure may not be directly related to the reaction, part of it is; the "active center" of an enzyme or the oxygen carrying region of hemoglobin are examples. These can't vary, but the rest of the molecule may vary quite a bit.The variable part of the molecule may have something to do with making the thing work in a particular type of organism.

The complete sequence is the ideal information to have available. Conversely, complete hydrolysis destroys the sequence and hence destroys the taxonomic usefulness of the protein. However, partial digestion of a protein, for example with trypsin, produces peptides which are homologous and which retain an index to the sequence. Thus different levels of protein structure can be utilized to investigate different taxonomic levels.

Now we can turn to the tecniques for comparing proteins. Electrophoresis is defined as the movement of charged particles suspended in a liquid, under the influence of an electrical field. Molecules which themselves have a charge will move of they are placed in the system and subjected to the effects of the direct current. They move at speeds which are primarily a function of their own net charge. The net charge is a function of the net charges of the charged amino acids. Not all amino acids have a charge. In a gel system, the size of the molecule also affects the speed of movement because of the frictional resistance

with the medium. Thus electrophoresis measures net charge and possibly molecular size, not the sequence of amino acids. Comparison itself becomes the important thing

What are advantages of electrophoresis? Speed, simplicity, and a body of comparative data that reflect something about structure. Electrophoresis reflects nothing about sequence. Differences in electrophoretic patterns are significant, but similarities are impossible to access in the absence of other supporting data. Similarities become important if other data also indicate close relationship.

Electrophoretic patterns should be viewed as morphological characters. They have some of the advantages and some of the disadvantages of gross morphology, which is subject to the same problems.

Another group of tecniques are those coming under the general heading of chromatography. Chromatographic tecniques, instead of taking advantage of net charge properties, take advantage of the solvent properties, or the ion exchange properties. These measure different characteristics of the same molecules. One of the powerful methods that can be used to measure both electrophoretic and chromatographic properties of the same particle is what we call "fingerprinting" or "peptide mapping". In this tecnique, a purified single protein is digested, for example, with the enzyme trypsin. Trypsin hydrolyzes the peptide bonds to the carboxyl sides of lysine and arginine residues. This specific enzyme will produce homologous peptides from homologous proteins. Another kind of peptide study can be carried out using oin-exchange chromatography, which produces complex curves for comparison.

Finally, it is also possible to determine the complete sequence of the amino acids in a protein. Present procedures are too slow for application to most taxonomic problems but there are hopeful signs that, within a few years, we will have automatic instruments capable of providing complete sequences in a practical length of time. Such data will give the systematist precise measurements of genetic relatedness and may truly revolutionize the field.

HYBRIDIZATION AND SYSTEMATICS

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Taxonomy is concerned with the description, identification and classification of the various kinds of plants and animals. The emphasis in taxonomy is on the pragmatic. Systematics is primarily concerned with populations of organisms, population dynamics and population genetics and through their study the elucidation of the processes of evolutionary change. The systematist attempts to ascertain, through the study of naturally occurring populations, if theocetical concepts of evolutionary processes conform to reality. My discussion will deal with the problem of hybridization from this latter view, the view of the systematist.

One of the difficulties with the term hybridization is that there are a number of different ways in which the term has been employed. From the genetic point of view, hybridization may be used for any cross which produces offspring with new combinations of genes, gene combinations different from those of either parent. In the present context hybridization will be used for mixings of gene combinations from populational gene pools that differ from one another in a substantial number of genes.

Three kinds of natural population systems exhibit hybridization:

1. Populations connected by continuous hybridization -

   allopatric contiguous

   ecogeographic races (ACER)

2. Populations connected by substantial hybridization -

   Sympatric races (SYR)

3. Populations connected by rare hybridization -

   sympatric semispecies (SYSS)

Figure 1 shows the distribution of two species of the toad genus Bufo in North America, that exhibit several degrees of populational hybridization. The two related forms and their named populations are:

Bufo terrestris		Bufo woodhousii
copei		fowleri
americanus		hemiophrys
charlesmithi		woodhousei
terrestris		velatus
houstonensis		
microscaphus	californicus	

In this series americanus-copei are ACER's; fowleri-americanus, woodhousii-microscaphus and fowleri-terrestris act as SYSS's. The distinctive characteristics of velatus are apparently the result of the incorporation of many genes from a third species Bufo valliceps into the woodhousii population of east Texas.

Bufo terrestris and its allies and Bufo woodhousii are best thought of as a pair of sympatric semispecies, with some hybridization between the two partially isolated complexes.

Hybridization between populations is prevented by isolatins mechanisms. In the case of ACER's these mechanisms have not developed. In the case of SYSS's they break down. Isolating mechanisms may be classified as follwos:

I Pre-mating (extrinsic) - external reproductive

1. ecologic - mates fail to meet
2. ethologic - mates meet but fail to mate
3. morphologic - mating attempted but no transfer of sperms

II Post-mating (intrinsic) - internal reproductive

1. gametic mortality - no fertilization
2. zygote mortality - fertilization no development
3. hybrid inviavility - F_1 with reduced viability
4. hybrid sterility - F_1 sterile
5. hybrid breakdown - F_2 sterile or inviable

Figure 2 shows the two possible modes of speciation (allopatric and sympatric). One of the key factors in discussing hybridization has to do with hybridizing populations related to one another in an evolutionary sense. There are several different theories which have been developed on how isolating mechanisms originate. First we see the history of populations that are differentiating by allopatric speciation. The process starts with one population and ends up with two sympatric species. These are the different levels; development of two ACER's from one population, disjunct eccogeographic races, allopatric semispecies, allopatric species. At the lower levels there is considerable genetic exchange. At the other end of the spectrum, after these populations have been allopatric for a long time, and they come back together, several things can happen, First of all, there can be complete genetic exchange (secondary intergradation) so that even after the period of allopatric isolation the result is continuous eccogeographic races. Or there can be a reduction in the genetic exchange so they are sympatric semispecies, or complete overlap without any hybridization to form sympatric species. What is going on during isolation that would lead to the development of isolating mechanisms? One hypothesis has been that while they are separated, differences in their characteristics develop so that when they come back together the isolating mechanisms have developed by chance. I don't believe this. Another idea that has been developed is that there are some facets of the isolating mechanisms that make their appearance during this period of allopatric separation but that almost invariably when the two populations come back together they behave

as in a secondary intergrading or sympatric semispecies relationship. When they first come back together, there is considerable hybridization but natural selection operates to eliminate the hybrids and very strong selection favors those features of the biology that will preserve the genetic integrity of the two populations. Hybridization could be a necessary precursor to the establishment of a strong isolating mechanism between two formerly allopatric populations. If this is true, then hybridization becomes an extremely important factor in the process of speciation, even in allopatric speciation. This raises the question as to what is actually going on in any particular situation. Is it the result of the development of isolating mechanisms when the populations are allopatric, or is secondary intergradation necessary for the formation of sympatric species?

Another way in which hybridization in important is in the development of apomictic populations in the vertebrates. In the lizard genus Cnemodophorus in a number of cases there are all female poplations which are in morphology distinct from allied populations. Investigation has proved the all female clones to be products of hybridization between two bi-sexual forms.

As an example (Fig. 3) the nominal species Cnemidophorus tesselatus is essentially all female. It occurs in the Rio Grande area through New Mexico and Colorado and Oklahoma. When herpetologists began investigating this problem it was discovered that tesselatus populations differ morphologically in color pattern and fall roughly into two color types, northern and southern. In the southern population, there is about one male in 400 specimens and in the northern population there are no males at all. It was proved that the southern population are diploids and the northern population are triploids. This is a fairly complicated case. The southern population has arisen from hybridization between two (tigris and septemvittatus) species. Both of these are bi-sexual, with males and females, their 2N chromosome number is 46. The karotype of the 2N population of tesselatus corresponds to the combination from tigris and septemvittatus. The 3N population involves a cross between the female of the southern tesselatus and males of a third species, sexlineatus (a diploid bisexual species) to produce 3N tesselatus which are all females. This is a case of hybridization that has produced an intermediate population in an unoccupied habitat.

Studies of hybridization between populations need to be centered on these two general evolutionary problems: 1)the role of hybridization in speciation, particularly in reinforcing isolating mechanisms; 2) the role of hybridization as a means of eliminating genetic contamination of species population through the temporary expedient of extablishing apomictic clones.

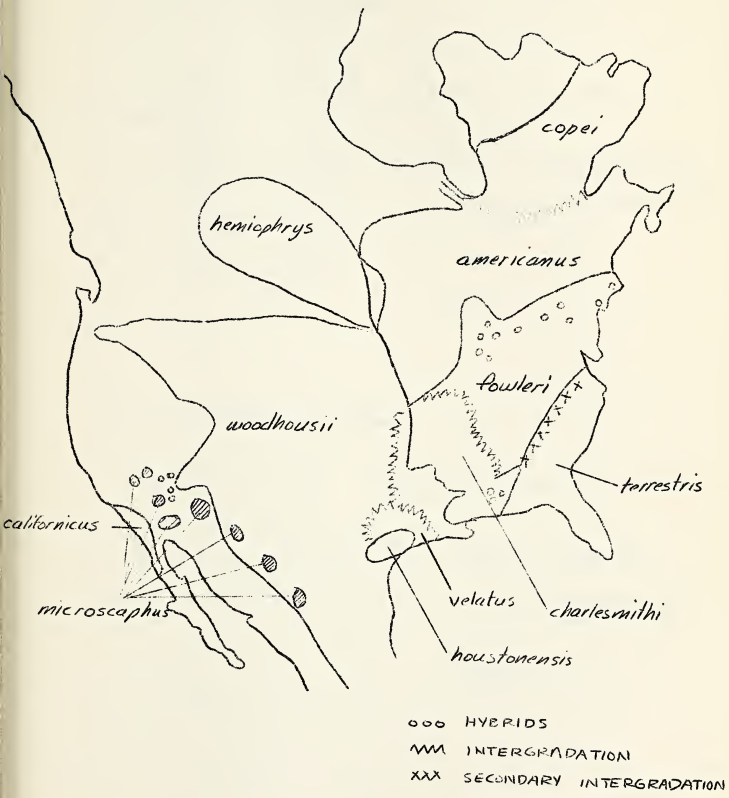
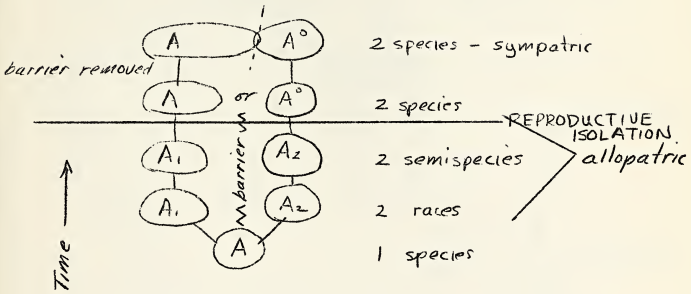

copei
hemiophrys
americanus
fowleri
woodhousii
terrestris
californicus
microscaphus
velatus
charlesmithi
houstonensis
ooo HYBRIDS
MM INTERGRADATION
XXX SECONDARY INTERGRADATION

Figure 1

KINDS OF SPECIATION:

A. *Allopatric Speciation*



B *Sympatric Speciation*

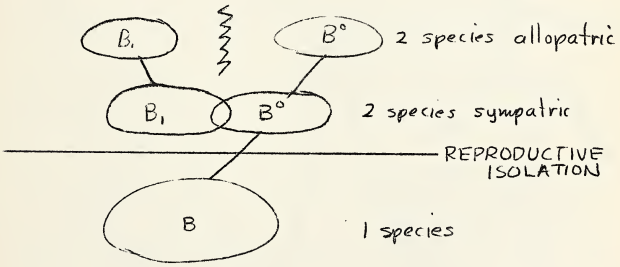


Figure 2

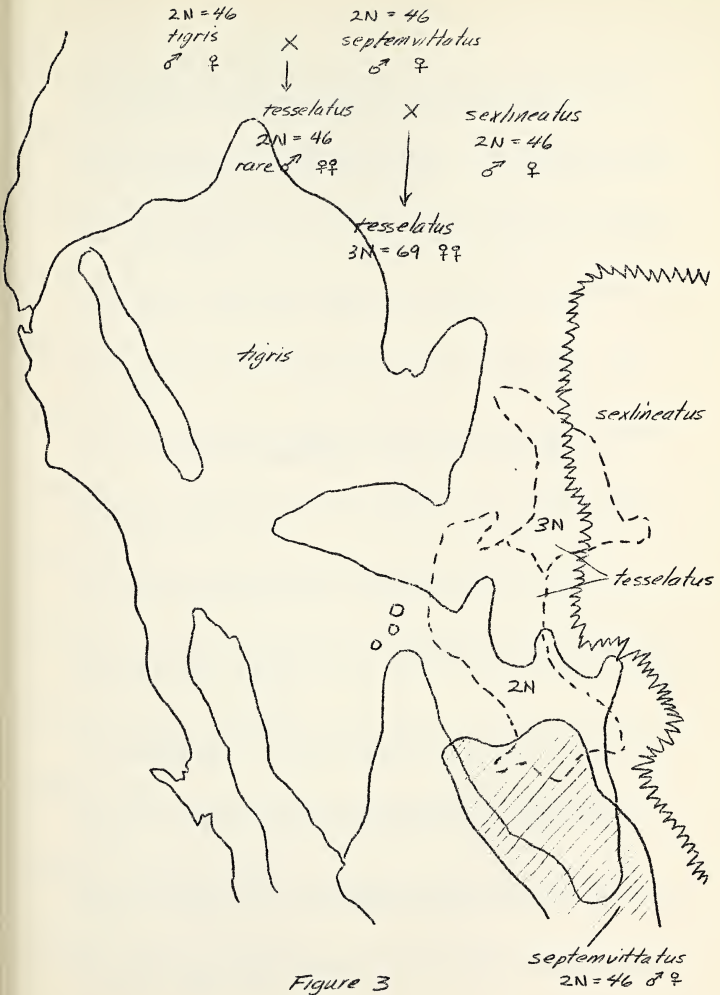

2N = 46
tigris
♂ ♀
×
2N = 46
septemvittatus
♂ ♀
tesselatus
2N = 46
rare ♂ ♀♀
×
sexlineatus
2N = 46
♂ ♀
tesselatus
3N = 69 ♀♀
tigris
sexlineatus
3N
tesselatus
2N
septemvittatus
2N = 46 ♂♀

Figure 3

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GENETICS AND SYSTEMATICS

Harrison D. Stalker

Washington University

The Uses of Chromosomes in Taxonomy

Considering first mitotic chromosomes, these may be used as an additional key character to distinguish species that are hard to recognize in other ways. However, profound intraspecific differences in mitotic chromosomes may exist, thus discovery of chromosomally different types may indicate different species, or may only indicate different races of the same species.

Similarly, species that are distantly related may show mitotic chromosome differences or they may not. Thus, the discovery of mitotic chromosome difference between two forms is not a reliable indication of taxonomic difference, and failure to find such differences is no proof of taxonomic similarity of the two forms. In some, study of mitotic chromosomes is often no more rewarding than study of any other variable characteristic as far as taxonomy is concerned.

I don't want to over-state my case here. In some forms, especially some plants, study of chromosome differences can be extremely valuable in revealing phylogenetic relationships, but such cases are not common, and generally the chromosome study, in order to be useful, requires the ability to cross the forms concerned.

In order to save time, I am not going to deal further with the study of mitotic chromosomes per-se, but consider the large banded polytene chromosomes found in the Diptera generally, and apparently absent from other organisms.

In the Diptera the large polytene chromosomes are found in various secreting tissues of the larvae and adult. For example they are known from the cells in the gut, malpighian tubules, nurse-cells of the ovary, and salivary gland cells. Structurally, these large chromosomes are generally thought to represent a series of uncoiled chromonema, with their chromatin masses, thus accounting for the great length, then duplicated as much as 1000 fold to give thickness, the chromatin masses lining up exactly to give the bands in the chromosome. Such chromosomes are as much as 100 times as long as mitotic chromosomes. Polytene chromosomes are ideally suited for taxonomic and phylogenetic studies for a number of reasons.

1. They have complex patterns, which are easier to analyze and describe than similarly complex patterns in morphological structures.
2. This pattern is relatively stable with time. Even though in the course of evolution the genes in chromosomes may under-go drastic changes, these gene changes are not as a rule reflected in the appearance of the polytene chromosomes. Thus quite destantly related species may show chromosomal banding patterns which are in part identical, indicating a very long pattern stability.
3. When patterns change, this is usually the result of simple inversions. Inversions are rare, so rare that the spontaneous rate

[illegible]

[illegible]

[illegible]

has never been adequately measured. The two breaks of an inversion can be accurately determined and mapped in polytene chromosomes. In favorable material, as many as 1000 recognizably different break points may be recognized on a polytene chromosome. Thus if a given inversion occurs, the probability that any additioal inversion will appear to occur at exactly the same places is about $(1/1000)^2$ or 1/1,000,000. Even in unfavorable material, if only 100 different spots could be detected, the probability that a second inversion would match an earlier one is only about 1/10,000. Thus a given inversion can be considered as a practically unique historical event. If two homologous chromosomes show the same inversion, it can be concluded that they inherited it from some common ancestor, not that it simply arose twice.

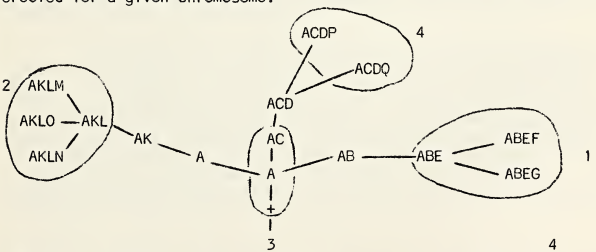
When a given chromosome suffers a number of inversions occurring one at a time, then it may be possible to work out the order in which these various inversions occurred. For example:

+	1 2 3 4 5 6 7 8 9 10 11 12
A	1 2 3 4 5 11 10 9 8 7 6 12
AB	1 2 9 10 11 5 4 3 8 7 6 12

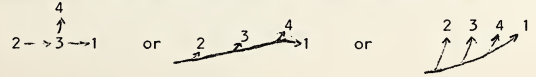
Here, due to the complex changes in AB, there is no way to go directly from + to AB in a single step by a single inversion. Since inversions are rare, and almost always occur one at a time, this means that chromosome type A is a necessary intermediate step in the change from + to AB or the reverse. If in flies in nature, whether in the same or different species, all three chromosome types are found, then we know that the evolutionary relationships are + ⟷ A ⟷ AB.

If additional inversions occur in the same chromosome, ultimately a complex phylogeny may be built up by this system of analysis. This type of analysis was first introduced by Dobzhansky and Sturtevant in 1938.

Suppose then, that using this method, a complex phylogeny is erected for a given chromosome.



Hanging the species on the chromosome phylogeny we get: 2 — 3 — 1 but with no direction indicated. This can be worked out in some cases. Suppose the indicated direction is to start with 2. Then:



Polytene chromosomes have been used in this way in the Diptera in quite a number of different forms, including mosquitoes, black flies, fungus gnats, Drosophila and a few other less well known forms.

Ordinarily the easiest way to compare the banding pattern of two homologous chromosomes, to see if they have the same banding pattern, or differ by one or more inversions is to bring them together in one individual by making a cross, and then since in Diptera the somatic chromosomes tend to show exact pairing of homologous sections, the two bhromosomes being compared will lie side by side, with the bands exactly lined up, and any differences can be easily spotted. Unfortunately this procedure won't work for most species comparisons because hybrids can't be formed, and the chromosomes must be compared by maps. In the early days (from the middle thirties) these maps were always hand drawn, they were beautiful to behold, but unfortunately extremely difficult to use, since such maps were made to show every band ever seen in a chromosome, and any given example of a chromosome is rarely favorable enough to show all the bands, thus the drawn maps didn't look too much like the actual chromosomes. More recently in our laboratory we started making photographic maps, and I am glad to say that this procedure seems to be spreading to other laboratories.

As an illustration of the use of this method, I want to talk about the phylogenetic relationships of one group of American species, the D. melanica group. This group is chosen because it is simple, because it has some interesting difficulties associated with it, and because having worked on it myself, I can talk about it more easily.

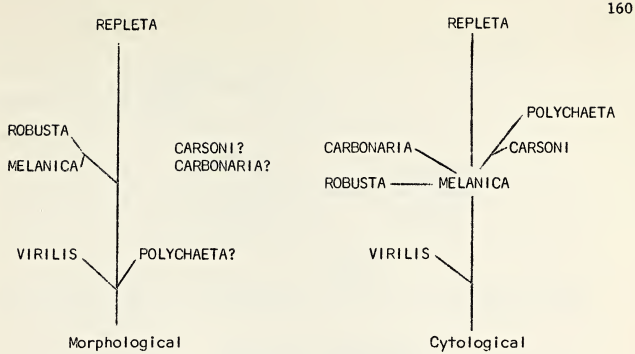
OMITTED: (Slides)

The Inter-Group Comparisons

The work on D. melanica was not an end-to itself, but rather a preliminary job to see whether phylogenies could be worked out by photographic maps, and to improve the technique as much as possible with a relatively simple group of species.

The major problem was to work out the inter relationships of all species of Drosophila, not just those belonging to the same species group. A word about species groups. In Drosophila taxonomy much of the work of the Texas group and of Sturtevant in California has involved the determination of closely related groups of species, the species groups. Hybridization may at times occur within groups, never between them. Knowledgeable insect taxonomists such as Sturtevant, Wheeler and Hardy in Hawaii have pointed out that these groups are sufficiently distinct so that in many families of insects they would be considered sub-genera.

OMITTED: (Slides)



Summary comparison of morphophylogeny and cytophylogeny.

Is such a phylogeny justified on parts of one chromosome? There is some evidence that it is:

1. In general it tends to agree with morphophylogeny. Any radical disagreement would suggest unreliability.
2. In those few instances in which the analysis was based on another chromosome, exactly the same phylogenetic relationships were indicated.

The Hawaiian Problem.

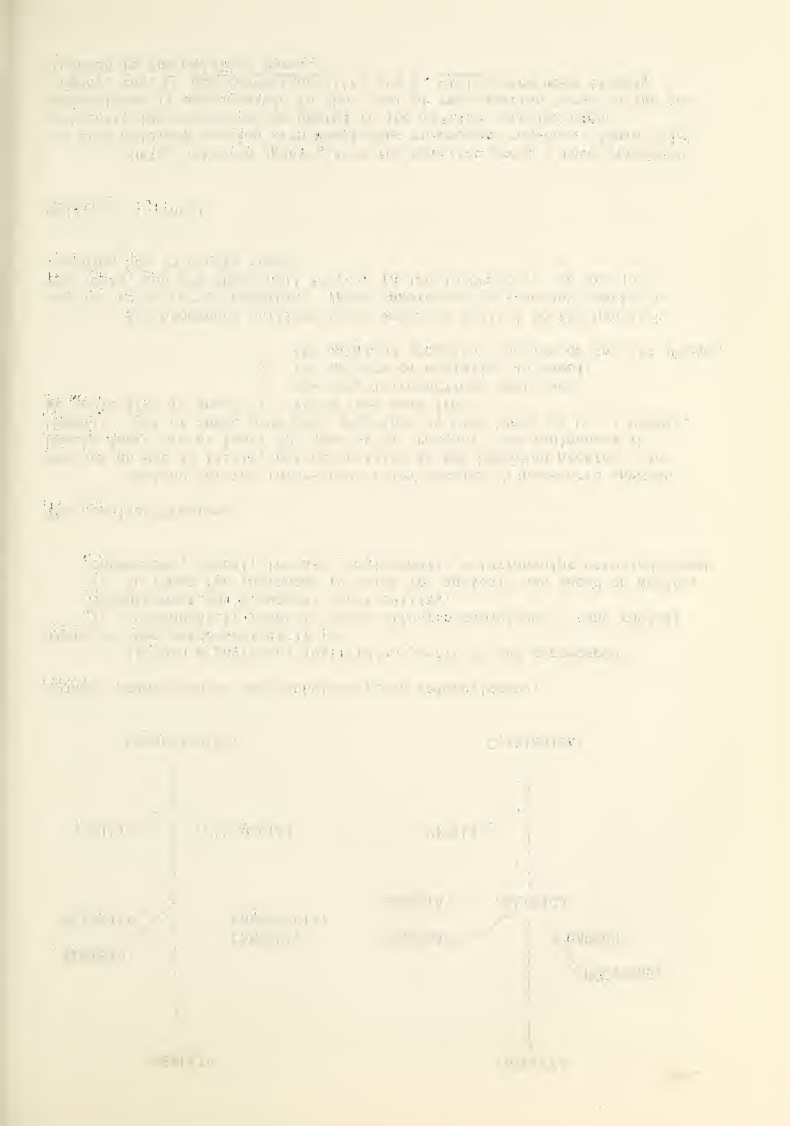
Working out the inter-group relationships of new-world species was not an end in itself, but was related to the Hawaiian problem. In Hawaii there are at least 300 species of Drosophilidae indigenous to Hawaii. Most of these have been described by Elmo Hardy at U. of Hawaii. We would like to know:

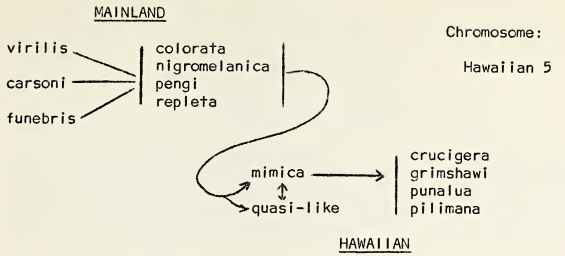
1. Where they came from
2. How many introductions there were
3. The pattern of evolution in Hawaii
4. The mainland ancestral species or species groups.

The procedure outlined above has been applied to the Hawaiian species in so far as possible. These species are unlike any others in the world, and are sheer hell to rear in the laboratory. We are just learning how to handle them.

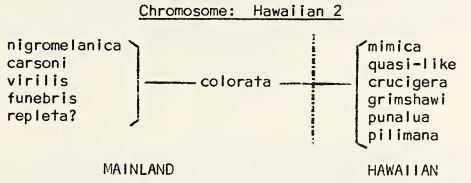
OMITTED: (Slides)

Using selected species from the Hawaiian group I have attempted to find mainland species with homologous chromosome regions. Again using primarily the chromosome so useful in the mainland species group comparisons it was possible to show that of the Hawaiian forms in the phylogeny, two, D. quasianomalipes-like and D. mimica were most closely related to the mainland forms.

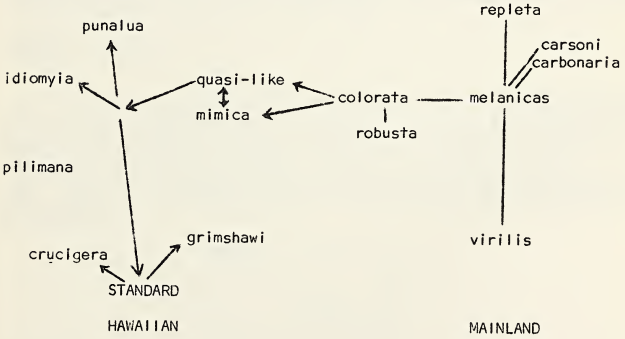




Of the mainland forms, D. colorata is closest to the Hawaiian forms.



Putting these facts together, the following relationship appears.



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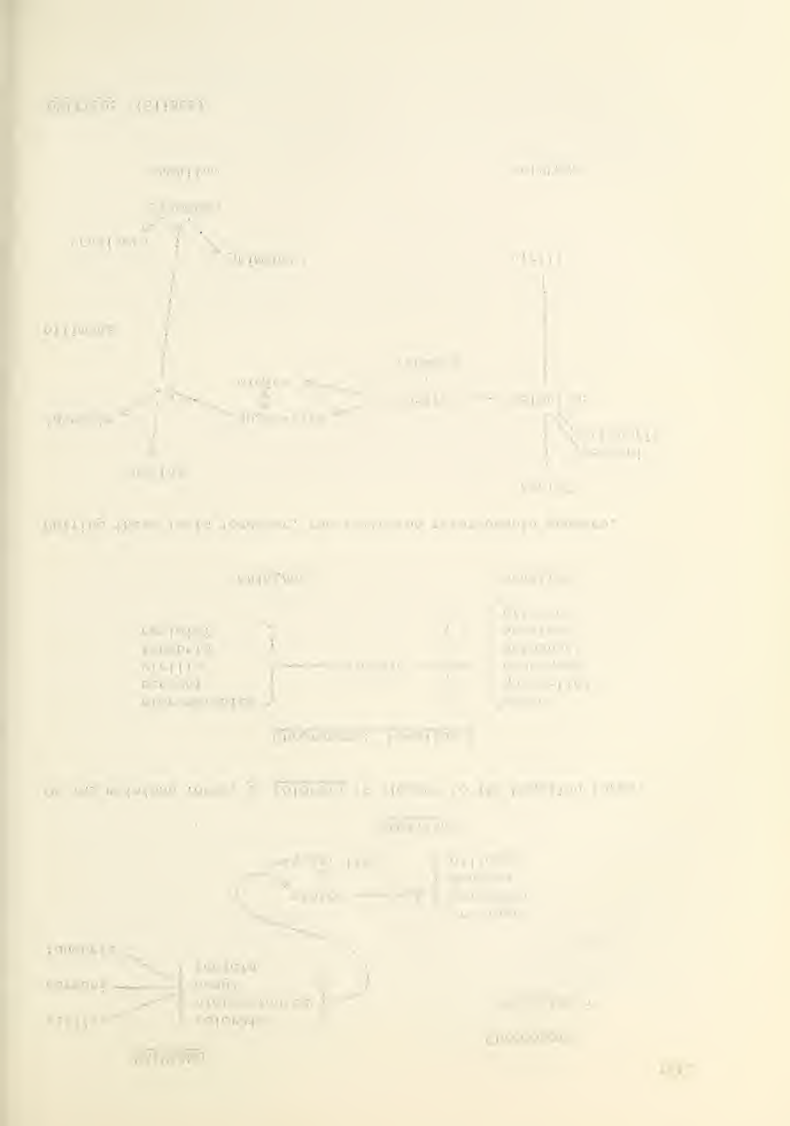


DISCUSSANT

Ellis T. Bolton

Carnegie Institute, Washington

Three years ago my colleagues Drs. Roy Britten and Michael Waring discovered that the DNA of higher organisms was comprised of polynucleotide sequences which were repeated, sometimes to an astonishing degree. This is a discovery, we believe, of no mean consequence for appreciating evolutionary mechanism, as I shall try to indicate.

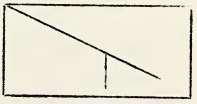
DNA is a duplex molecule composed of complementary strands held together by H-bonds and other weak forces. These forces are readily lessened by simple means such as heating, which confer disorder to the system and permit the exactly associated strands to part. Once parted the strands can be kept separated or can be induced, by appropriate manipulation of test-tube conditions, to come together again. These events are schematized on the first slide.

OMITTED: (Slides)

It is obvious, thus, that strands from the same or from different organisms can be induced to behave in this way, and that, again using appropriate technology, one should be able to determine how many nucleotide sequences organisms hold in common. That is, he should be able to detect genes in common among diverse species and to circumvent the barrier of reproductive isolation usually insurmountable for such purposes. A result of such studies is shown on the next slide.

OMITTED: (Slides)

This is a satisfying empirical result--it fits with the textbooks. It is not very controversial. In addition, it gives a quantitative feeling for what the vertebrate systematist means by the taxonomic categories he uses. It also permits us to put a time-scale, through studies of contemporary creatures, on events which must have occurred in the distant past. Here we are indebted to the paleontologist and the geo-chronologist for an abscissa, and to the molecular biologist and physical chemist for an ordinate.



10^8

This is an extraordinary bit of systematics. It says that half the genetic material of an organism changes so as to be unrecognizable by another creature's DNA in a period of 100 million years. Or does it? This is the question to which Britten, Waring and Kohne have addressed themselves. To get at it they asked, "Precisely what is occurring in these interactions?"

(1) The reactions occur between long nucleotide sequences. In the case of virus DNA, "good" duplexes are formed upon reassociation. But a virus is genetically simple--it may contain only 100 genes or less. The empirical fact is, that with this order of complexity, DNA duplexes of good conformity can be induced to re-form.

Even for bacterial DNA, which is much more complicated, "good" duplexes are re-formed. The bacteria may contain tens or hundreds more different sequences than do viruses. But for an equivalent amount of duplex reformation, since the reaction is bimolecular, it should, and does, require a far higher concentration of interactants, or a longer time, or both, other considerations being equal.

But the DNA of higher organisms is, presumably, another ten or hundred or hundred or thousand times more complicated, and inordinate concentrations or reaction times would be required for equivalent results. This consideration, in view of the empirical results presented, poses a question: Is the DNA of higher organisms really all that more complex? Certainly it is shattering to our ego to think we are not al least a hundred or thousand times more complicated in our fundamental genetic make-up than the enteric bacteria we harbor (!)

I have put at the end of that statement an exclamation point in brackets, which reminds me of an "Ode to Modesty". It goes:

> "Talking of successful rackets
> modesty deserves a mention.
> Exclamation marks in brackets
> never fail to draw attention."

(2) Is there a fundamental difference, perhaps, in the construction of the genome of higher organisms as compared to the viruses and bacteria? The answer is yes, and is shown by a very simple experiment. One merely incubates single-stranded DNA from a higher organism, then centrifuges the preparation at relatively low speeds. Under appropriate conditions nearly all the DNA will sediment as a compacted gel.. This is not the case for viral or bacterial DNA. In order to form a gel--which is a three-dimensional interconnected network of molecular strands--the strands must contain multiple regions of sequences of nucleotides which are similar enough in complementarity, and frequent enough in occurrence, to provide for the interactions that lead to a three-dimensional structure. Patently, viruses and bacteria do not have such potentiality. All eukaryotic organisms so far examined exhibit the requisite repeated nucleotide sequences.

OMITTED: (Slides)

What might be the origin and significance of repeated nucleotide sequences?

A clue is given by the rediscovery of the so-called mouse satellite DNA. This DNA is a most reductant collection of polynucleotide sequences numbering perhaps 10^6 for each mouse nucleus and comprising 10-15% of its DNA. It is recognized by its extraordinary rapid rate of reassociation, by its sedimentation characteristics and by its separability from the majority of the mouse DNA. It also has the interesting property that 2/3 of its pyrimidine residues reside in one of the sister chains, while 2/3 of the purine residues lie in the other.

The simplest explanation for its existence is that it is a new evolutionary invention having arisen as a saltatory event by a linearly redundant biosynthesis. The rat does not contain such a satellite.

On the other hand, it may be striking only because it occurs in such large amount--it may only be a relatively bizarre example of saltatory events of a similar nature which are occurring to a greater or lesser degree among all higher forms all the time. What is evident from data already in hand is that all higher organisms contain extremely rapidly renaturing fractions of DNA. The following slide shows some data relating to the rate of reassociation of various DNAs.

OMITTED: (Slides)

What is a Saltatory Replication?

The appearance in the genome of a family of repeated sequences involves a number of events: (1) Many copies must be made of a segment of DNA; (2) a number of these copies must be integrated into the genome in such a way that they are duplicated and transmitted to progeny; (3) the resulting family must either determine a favorably selected phenotype or be associated with a favorable genetic element; (4) sufficient time must pass for its dissemination throughout the population; (5) if the set of events can be described as a saltatory replication the growth of the family must be terminated within a reasonably short time.

No known processes combine all five of these events. Virus infection, however, does involve some of them. In virulent infection very many copies are made of the virus genome. In a lysogenic state a chromosomally integrated segment is transmitted to progeny. Further it is known that segments of DNA which are capable of genetic activity in the host may be, in some living systems, carried in the virus' life cycle. Cases are not known where large numbers of viral DNA copies are integrated into the host genome nor are any cases clearly established in higher organisms where new host-type genes are carried in a virus life cycle.

We are not proposing that saltatory replications are the result of virus infection but the relationship may suggest new experimental approaches. There are several cases in which a quantity of DNA results from the production of many copies of particular segments of DNA: The tremendous quantity of DNA (mainly mitochondrial) in certain eggs; the mitochondrial and chloroplast DNA in more typical cells; DNA puffs in insect chromosomes. In none of these cases is it known that the copies may become integrated in such a way that their descendants are transmitted to the progeny. Such an event is necessary in order that the members of a repeated family may diverge from each other. Only the small fraction of the repetitive DNA which does not show divergence (having high thermal stability after reassociation) can be DNA which has been recently replicated from a master copy.

Events of this general type would be capable of causing a striking divergence of two genetically isolated populations even though the environments in which the two populations existed were identical.

The wide occurrence of families of repeated sequences and the implication of saltatory events in their production as well as in evolutionary processes indicates that sudden events may be far more important to evolution than we have heretofore suspected.

Thus, a hierarchy of commonness in the construction of the chromosome emerges in a new guise--one at the level of informational sequence, rather than at the level of what the light microscope can reveal, as you have heard at length today. Here lies a common ground between Dr. Stalker's researches and those my colleagues and I have been conducting. But it is ground so new, and so unexplored, that there has been no time to see even its first fruits. I hope that between us, Dr. Stalker and I have been able to plant a few seeds which will come to fruition. What is clear, I think, is that this area is most promising, and that its exploitation will require the talents of the geneticist and the evolutionist, the cytologist and the physicist. Systematics is, as Dr. Mayr quoted, the science of 'the diversity of life' and it requires diversity of discipline.

CLASSIFICATION

R. E. Blackwelder

Southern Illinois University

I have rather a privileged place here today, at the end of your consideration of theoretical aspects of taxonomy, and I might use it for rebuttals to some things previously said. I'm sure this would be unfair, and I'll avoid it where I can, but it's not reasonable for me to discuss classification with you without giving you a clear view of differences in philosophy and in the use of some terms.

In his address at the beginning of this series, Dr. Mayr seemed to expect later speakers to disagree with him. This is scarcely necessary in my case, as he and I are talking about different things. Much the same applies to the remarks of Dr. Sokal and other speakers; if we can as a group grasp clearly the concepts and framework they use, we find that controversy melts into mere non-communication due to different viewpoints.

I feel I must apologize for seeming to dominate this session with a new book that is rather broadly relevant to the subject of this institute. I didn't plan it that way, as publication was much delayed. But you'll understand that after five years of working on this book, I'm not going to come up with much here that hasn't already been said in the book. The ideas I'm going to offer you are all there, but widely scattered, and without some of the illustrations.

I'm not an extemporaneous speaker, and although I have worded and reworded these ideas many times in various drafts of the textbook until they should be second nature to me, I still like to be sure I get just the right wording. The only way I can do this is by sticking closely to a script.

Classification has been referred to by most of our previous speakers. It has sometimes not been quite clear to me what they meant by the word, and it has seemed as if arrangement in a system was to them only a means to some other end. In my opinion, classification by itself is not only an important part of taxonomy, but it is THE major scientific activity of the field. Without it, the rest of taxonomy would be virtually useless.

One distinquished systematist, in expressing this same view of the importance of classification, concluded that all other work done by taxonomists must be unscientific, mere sorting and cataloging. I want to make it quite clear that I do NOT subscribe to this conclusion. In a few well-worked groups like the higher vertebrates, it's hard to see the importance of the segregation and description of new species and genera. But in large parts of the Animal Kingdom no classification can be done effectively until much more descriptive work is done. If the descriptive taxonomist is working toward the general goals of taxonomy, his work can be important even if he never gets a real chance at higher classification.

One reason why classification as such was slighted on this program may be that it's so little written about that it would be hard to assemble speakers. I have found this to be one of the most difficult aspects of taxonomy to deal with, but one of the most necessary ones. Another reason is that various definitions of the terms have left misunderstandings.

We'll have to specify how these terms are to be used.

The people who call themselves taxonomists do a variety of things in the course of their work. Some do mostly one thing, some mostly another, and some do a variety of them. For example, taxonomists collect, prepare, curate, and record specimens; they identify and label them; they describe species, write keys, and compile catalogs; they study previous literature; they propose and apply names, using complicated rules of nomenclature; they classify species into groups and the groups into more-inclusive-groups. They may prepare monographs which involve all of these activities in a united effort. It should be possible to separate these activities under suitable words.

There have been several definitions of the available words in this field. In all such sets there are some things included that are not part of the ordinary work of most taxonomists, but are part of a broader field encompassing other specialists also. It seems to be nearly universal to use the word systematics in a broad way, to encompass taxonomy, arrangement of species into a classification, the study of phylogeny, and even the study of evolutionary processes. Systematics thus is the study of the kinds and diversity or organisms, their distinction, classification, and evolution.

Approximately this definition has been quoted to you by several speakers as that of Simpson in his 1961 book. It didn't originate with him, having appeared ten years earlier in volume 1 of Systematic Zoology. It is substantially the definition given by Ferris in 1928 in his classic book Principles of Systematic Entomology.

The word "taxonomy" has sometimes been used in this broad sense, as in the three stages called alpha-, beta-, and gamma-taxonomy, to which Dr. Mayr referred earlier. Alpha is segregation and description, beta is grouping or classifying, and gamma is the evolutionary part. These would be more appropriately called alpha-, beta-, and gamma-systematics.

Taxonomy can only be defined, it seems to me, as the work that the taxonomists do. Any other definition makes it meaningless for such men as are in the Museum here to say that they are taxonomists, as many of them do. (Of course, they're all systematists, too.) The vast majority of taxonomists---(By the way, did you ever see Dr. Simpson's comment that it's very easy for a person to mistake himself for a majority? In this case, I'm not referring to myself but to the people I think I know well in this regard.) The majority of taxonomists, then, are busy with the discrimination of genera and species, the naming of them, and the publication of studies about them. Many taxonomists spend their entire life at these important tasks. So taxonomy is the day-to-day practice of dealing with the kinds of organisms.

The third word we need is the same as the beta-taxonomy, although that expression has recently been assumed to comprise part of the evolutionary studies, which it did not originally do. Classification is the arrangement of the species into groups and the groups into a system. The system is also called a classification. The data about the kinds determine their position in the system and thereafter are reflected by that position.

Several speakers have suggested that Simpson defined taxonomy as being the same as classification. But this is a misunderstanding. His formal definition gives taxonomy as the study of the THEORETICAL ASPECTS

of classification, the philosophy of systematics, the metataxonomy or methodological taxonomy. Under this definition, no one here and probably no one in Washington would be a practitioner of taxonomy, concerned primarily with the philosophy of classification. But Simpson. who is beyond all doubt a distinquished systematist, didn't follow his own definition; he used the word "taxonomy" to refer to the discrimination and classification of species. At least, he used it that way in the text; in the title of his book he used it in the philosophical sense as defined.

It's not intended to imply that these words represent completely distinct activities. We will here be concerned mostly with classification, which is the grouping of like things into a system.

There is one thing that I must make clear, even at the risk of arguing with some other speakers on this program. The classification to which I refer is based on attributes of the individual organisms. It is NOT based on their ancestry, their phylogeny. It may contribute to our knowledge of phylogeny, but we classify first. I've never seen a classification based on phylogeny, although I've been challenging Dr. Mayr and other evolutionists for years to produce examples. (We'll talk more about that later on.)

What, then, are the uses of classification? Why do we classify? What are our goals in classifying?

At its beginning, taxonomy was concerned mostly with distinquishing species. This work continues because in animals in general new species have never been described as fast as they were collected. But it would be a mistake to leave the impression that recognition and description of new species is the only, or even the primary, purpose of taxonomy. This is only a prelude to the major job, which is classification. We may forget that the most difficult part of taxonomy is that of keeping track of all the information discovered. Because there are at least a million kinds of animals, it's a colossal job tokeep track of hundreds or thousands of facts about each kind; keep them available in a way that will permit extrapolation from them; and arrange them in a system that will permit unlimited additions of new data at any time.

The first requirement is a system of classification by means of which the kinds can be kept in order. An alphabetical file would serve admirably for this purpose, but taxonomists have found that a great deal of additional advantage can be obtained if animals with like features are grouped together into classes at various levels in a hierarchy. This was one of the ways known to the ancients for handling and increasing knowledge, and it's a normal part of the subject matter of Major Logic, which deals with definition, division, grouping, and argumantation as instruments of knowledge.

In spite of the view expressed by Dr. Mayr, that the logic of Aristotle and Linnaeus is now outmoded, no way has been suggested in which they are either inadequate or have been superseded, in spite of the irrelevant reference to that bogie-man, the so-called typology-- a thing which in my opinion never has existed as a real factor in taxonomy.

Specifically, the goal of taxonomy is to build and maintain a classification and naming system capable of identifying and grouping all the kinds of animals that exist or have existed; to keep it consistent with all the facts discovered about animals; to use it to organize all the facts available; and to elicit new facts about correlations and groupings. Its basic purpose is thus to systematize data for the use of all

disciplines of biology and to uncover new facts in these data themselves.

These purposes don't complete the story. As shown on your outline sheet, in addition to recording data about kinds and producing new data through correlation, observation, and analysis, classification makes possible identification, prediction of the state of unrecorded features, conclusions on phylogeny, and explanations of the diversity of animals. Successful use of a classification for any of these from (2) to (6) depends upon the extent of the first; maximum information content will permit maximum deductions to be drawn and will also insure maximum stability of the classification.

The first task of a taxonomist is to make the species of nature known, and the second task is to arrange them into a classification, which will then yield the six benefits listed.

What form do classifications take? Here is an example in which part of a classification down to genus is shown. It's obviously impossible to include much on such a simple diagram. Part of this information is shown here in different form. This has been called the "classification" of this species, but that's a misleading phrase. It's better to call it the hierarchy of taxa of this species.

Another example is shown here. But note that this one contains an error--three times. There is no species known as domesticus, lupus, or mellifera. You must repeat the name of the genus, as here again.

A completely different form of classification is shown in the pie diagram, in which the entire circle represents the highest level in the hierarchy, the subdivisions the next level, and subdivisions of any of these would be a third level. (A variety of actual classifications will be illustrated in our second session later this morning.)

There has been great pressure on taxonomists in recent years to accept certain ideas as basic to their work. Some of these ideas have been of a peculiar nature which led Woodger to call them "acceptances". In Woodger's words, an acceptance is a system of statements which cannot be shown to be true but which is helpful in satisfying some need. Although not proved, it is believed in so intensely as to become dogma and to generate vigorous verbal acclaim. Its falsity can be shown only by careful analysis of all premises and their logical consequences. There may be some difference of opinion as to whether something is an acceptance or not, but lack of thorough justification for any idea can arouse suspicion.

An example of an acceptance is homology based on common ancestry, that is, recognized because of common ancestry. It has not been proved and cannot be, yet we continue to act as if it is logical and reasonable. We WANT to believe it, so we do. As a matter of fact, as one of our earlier speakers pointed out, we can get just as much benefit from homology by defining it as correspondence based on position, structure, development, and so on.

In the statement about the goals of taxonomy, you may have noticed that I did NOT say anything about a natural classification. This is one of the subjects which I would prefer to leave until later in our discussion, but it seems to require our attention early because it is another of these acceptances. What I'm talking about is the distinction between artificial and natural classifications.

Various authors have defined a natural classification to be:
one that seeks to show the blood-relationships
one based on the probably evolutionary relationships
one that groups those which are related to each other through common ancestry
one that has a basis in phylogeny
one that relies on phylogeny
one that conforms to the available knowledge of genetic relations
one that reflects the objective state of things
one that more truly reflects nature
one that enables us to make the maximum number of prophecies and deductions
one that groups so as to place together those with the maximum possible number of attributes in common
one that reflects the objectively ascertainable discontinuity of variation
and one in which the objects resemble each other in a multitude of particulars and appear to be grouped together by Nature

These are approximate quotations, and the list could be extended almost indefinitely. These authors had only one thing in common- they all believed that biological classification should be natural, as they understood that word. If the list were extended at random, it would become obvious that recent writers overwhelmingly include phylogeny as the basis in their statements. The commonest statement is probably that a natural classification is one that groups those which are related to each other through common ancestry.

Only a few of these writers were dealing with theoretical aspects of taxonomy. Most of them are quoting in their textbooks the statements which they have read in other works.But an increasing number of thoughtful systematists are questioning those requoted statements and asking for convincing argument that provides a logical basis for the definition. Such argument is simply not forthcoming, and many biologists are trying to turn to a more logically defensible definition.

The nature of the challenge is shown by the one based on probable evolutionary relationships, which admits that the ancestry is never known but only inferred. Some of the others beg the question by depending on such indefinite expressions as "reflects nature" or "the objective state of things." The fallacy of assuming the phylogeny is ever really known makes certain of these definitions illogical, and there are left as justifiable only the ones grouping on the possession of attributes in common (similarities, preferably many of them) and those with grouping based on the discontinuities in the diversity.

All modern philosophers in the field of biology, as distinguished from taxonomists themselves, seem to be agreed that there is no possible basis in common ancestry because this common ancestry is never known as a fact, that correlation of attributes is the only natural method of classifying, and that this method will prove to be the most useful in taxonomy. They don't say that a classification should NOT be natural. They're saying that the most natural classification possible is one based on many direct attributes of the specimens or taxa. (And some of them believe that such a classification will give us the best information on the possible course of evolution- the phylogenies.)

It's further denied by some recent writers that it's even possible to make an independent classification of any animals based on phylogeny.

It's impossible, first, because phylogeny is not known but merely hypothesized, and is therefore not an attribute, and, second, because the phylogeny(whether real or imaginary) is based on previous classifications. Inasmuch as all animals being classified NOW are known to some extent, the supposed phylogeny is based on the known facts. It would be a false argument to then say that a classification based on the supposed phylogeny is independent of the same characters that were used directly in the conventional classification on which it was based.

No one denies that evolution produced the kinds we are now classifying. No one denies that the sequence of forms through which a particular species arose is in fact a phylogeny of that species. No one denies that some of the features of the animals are the result of the phylogeny--the result of descent from an ancestor which possessed those same features. And no one denies that some of these features are good characters for classification. What is denied, here and in several recent books, is that the phylogenies are ever really known.They are only postulated. The best of them have been changed recently and are apt to be changed again. And there are no examples of classifications actually based on what were taken to be phylogenetic facts as distinct from the features of the animals.

With this situation, there is only one way to define a natural classification consistent with the known facts and useful in systematics. A natural classification is one in which the groups are recognized by having a maximum number of attributes in common, with their limits set by discontinuities in the diversity, and capable of yielding the maximum number of correct deductions about correlations of other features. It's possible to express this less explicitly by saying that a natural classification is one which reflects the most of the various natures of the objects.

Artificial classification, as usually contrasted with natural classification by the phylogenists, is simply one that was not based on evolutionary relationships. Under this definition, ALL our classifications are artificial, in reality. The usual example cited is the classification of books in a library. The example is entirely irrelevant to biological classification. Furthermore, a classification of books by subject could be natural, because the subject matter of books is a basic feature of their individual natures. With the definition I'm accapting here for natural classification, artificial classification becomes simply one that is based on so few characters or such illusory discontinuities that it's not capable of producing acceptable deductions.

If you have occasion to refer to classification based on common ancestry, why not be explicit and call it phylogenetic classification? The expression "natural classification" no longer clearly involves a basis in a known common ancestry and will surely be misleading.

This line of reasoning may be new to you, but it has been propounded by Gilmour, W.R. Thompson, and others for three decades at least. You may be astonished to know that it's most clearly stated by Simpson, who is a confirmed phylogeneticist. Some people seem to have misread Simpson, or perhaps they assume that his 1961 book is better than the 1945 one, which is not always the case.

Simpson gives the most reasonable and complete discussion of phylogenetic classification of any recent writer. He denies categorically that a classification does or can express phylogeny; he denies this and he describes the "primary purpose of a classification" as "simply to

provide a convenient, practical means by which zoologists may know what they are talking about and others may find out." Many of his readers seem to have overlooked these forthright statements, preferring to take note of a later sentence that SEEMS to contradict the first:"The basis of this system", he says, "is phylogenetic, as has been strongly emphasized here, and this means that the groups to be recognized in classification should be as nearly as possible valid phylogenetic entities and that the criteria of definition are to have phylogenetic implications..." Thus, the basis is conceptually phylogenetic, but the groups are not based on phylogeny.

These same readers fail to note the implication of still another statement: "Phylogeny must itself be determined before classification can be based on it." As a paleontologist, working with sequences of forms that are interpreted as giving data on phylogeny, Simpson apparently believes that there ARE phylogenies known, although he admits that none is perfectly known and universally accepted in detail. In fact, for it to be possible today to claim that there are phylogenies known, one would have to define this word "phylogeny" as the supposed or postulated history of the species. If it is defined as the actual history, surely there are none that could qualify.

We need to make a clear distinction between THE phylogeny of a species, the course which its evolution did actually follow, which we may be trying to determine, and the sequence which we POSTULATE may have been that evolution.For theoretical purposes we can talk about the actual phylogeny, even though we don t know what it was. But when we start drawing conclusions from this history, we must recognize that we're concluding from the postulates we make as to what the actual course of evolution was. And this is scarcely acceptable logic.

The idea that classification must show the phylogenetic relationships of animals was referred to by Raymond Pearl in 1922, when he denied the common view that the evolution theory MUST have an effect on taxonomy. This is another acceptance that is popular today. The evolution theory simply has not had the expected effect, although many aspects of evolutionary study have contributed to the advance of taxonomy and have contributed some data of importance in classifications. But the fact that we concede that evolution has taken place and that therefore at least some animals are related by descent to some others does not forse us to use genealogical relationships as the basis of our classifications. And although this has frequently been stated to be a logical necessity, which it is not, there apparently have been no cases in which a classification has actually been proposed solely on the basis of a pre-established phylogeny.

It was truly said of classification that "its value lies solely in the aid which it can give in the understanding and the interpreting of the facts which it reveals." And one of its points of aid is in supplying inferences and data on which we can base the speculations about phylogeny. It was Ferris in 1928 who wrote this, and he recognized that the more data there are available for the classification, the more aid it will give us in various applications. The aim should thus be to make the classification, as he said, "display in the most advantageous and most nearly correct manner the facts that have been discovered." This will include all facts of whatever nature, even phylogenetic.

The classifications now in use are all "natural" in the only useful meaning of the word. They can be made more and more useful, and will be,

by incorporation of new data whenever such become sufficiently available. This includes even phylogenetic data, but at present there are no useful data of this sort, because the correlations obtainable from the phylogenetic inferences that are obtained from other data have already been utilized in the system under the guise of structure, distribution, ecology, physiology, and so on. Any attempt to distinguish between phylogenetic and artificial systems will do nothing but confuse the true nature of natural classification that reflects the maximum of all the natures of the subjects. Such confusion would delay the improvement of the useful natural classifications, still based largely on structure and increasingly on data from all other fields of biology.

It's greatly to be hoped that taxonomists will not be so attached to the "acceptance" represented by the phylogenetic basis of classification that they will fail to recognize its true position as just one of the possible natural systems, one at present completely unattainable, and one not yet demonstrated to be even theoretically superior to any other. Taxonomists need not fear that they will lose anything by recognizing this state of affairs. They will actually gain several important things: first, freedom from the confusion of believing in and aiming at an unattainable goal; second, a practically as well as theoretically justifiable basis for their important scientific work; and third, a start toward the recognition that rigor in language is a factor of tremendous importance in a field as complicated as taxonomy. Language should be our servant. We mustn't allow it to be our master, overpowering us by means of the notions attached uncritically to words.

It's impossible to discuss classification usefully without a clear understanding of the words species, genus, group, taxon, hierarchy, category, and concept. You're already well aware that there's misunderstanding of some of these due to varying usage. I find little difficulty in defining most of these simply, in a way that seems to suffice in these matters before us today.

There are two ordinary English words that are at the base of all taxonomy and classification. These are "kinds" and "groups".

It has been known from ancient times that each sort of animal reproduces itself, producing others of the same sort. These are KINDS, the animals which can interbreed and produce more of the same kind (or produce more by asexual reproduction). A kind includes all the individuals that might have been produced as offspring of one pair or parts of a clonal colony. Even before there was much knowledge of heredity and its mechanisms, it was obvious that kinds consisted of the animals that were or could have been related by being descendents of similar individuals. This is the same concept which is now called more technically SPECIES.

Groups also were recognized in ancient times. Any two or more kinds that are placed together figuratively because of some characteristic held by all of them are a group. The term is both general and specific, as it can be used effectively to refer to the group of aquatic animals with fins or to the group of kinds of birds we know as sparrows.

Groups may consist of a set of kinds or they may consist of a set of groups. The groups that are called individually sparrows, woodpeckers, warblers, herons, and so on, which are groups of kinds, will altogether be the group called birds. And the group called birds, along with the group of mammals, the group of reptiles, etc., will be the group called

vertebrates. Thus, group is a noncommittal word, not specifying the number of its members or even whether they are individuals, or kinds, or groups of kinds.

If the group is a taxonomic one, as in these examples, then the word "taxon" is a synonym of "group". Taxon was first used by botanists and is now frequently used by zoological taxonomists. In taxonomy, any group is automatically a taxonomic one, and thus a taxon. (This is a good word, for which we can be grateful to the botanists. It helps me forgive them for that confusing pair, monoecious and dioecious, which they gave us a few years ago, but which cause students so much trouble.)

It's possible to arrange kinds(species), groups of kinds(taxa), and groups of groups(also taxa) in an ascending series of even greater inclusiveness. But before we talk about the hierarchy of categories I want to deal with another problem.

It has been said that all the taxonomic groups are mere concepts or mental constructs. I've never been able to understand this viewpoint. When I put five books out here together, they form a completely objective group. If I take one away, there is still an objective group. I suspect that this idea is parallel to the claim that taxonomists actually use hypothetical morphotypes. If they did, their groups would also be hypothetical. But morphotypes aren't consciously used, and the groups are always real and can be made clear-cut by proper restriction.

The real problem here is misuse of the word 'concept', and a few minutes taken to define that word should be worthwhile.

A concept is an idea in the mind of a person. It results from sense impressions and imagination. It's the mental picture seen at the time and remembered. It exists only in the mind of the one individual, for there is no direct way to communicate concepts. By converting the concept into a statement, verbal or pictorial, one can induce another person to form a concept from the statement. In the case of concrete concepts, those representing objects, it is sometimes possible to compare two concepts(in two different minds) by comparing the statements about them with the objects and reach a degree of certainty that the two concepts represent the same thing. (example of lecturn) In the case of abstract concepts, those representing classes of objects, hypothetical objects, and transient phenomena, there is no way to compare the concepts of two individuals, no way to be sure that they are the same. The nearest approach to assurance is by defining the terms used in the statement by reference to other concept-statements previously agreed upon. All language is based on such definition.

It's unlikely that any two individuals have exactly the same concept or idea which they associate with any given term. Their ideas are always colored by their past experience. It's therefore ineffectual to speak of a concept held by many persons, such as "the biological species concept." We can only study the statements made about the concept, and it's possible for many persons to express agreement with the statements. Unless each statement is completely free os ambiguities, however, there can be ne assurance that the individuals are agreeing to the same thing, because they in turn agree only to the new concept they have formed from the statement, and any ambiguities will lead to different ideas of what the statement means. The use of the term "concept" in place of such a term as "definition" serves to obscure the nature and source of the information or ideas under discussion and to prevent logical treatment

of the statements.

Inasmuch as concepts can be known to others only through the statements made about them, the statement becomes the thing that is important whenever concepts are involved in science, because there can be no science without communication. It must therefore be understood that when the word "concept" is used in a general sense, the actual object of reference is the statement derived from the concept. Only the statement can be examined; only the statement can be judged as to accuracy, truth, or agreement with other statements.

Groups, by which we mean groups of objects of groups of groups, are not at all like concepts. They may arise from concepts, from sense impressions, but they can be entirely definite if the features setting them apart are clear-cut. The groups may be of any size; they may be founded on intrinsic features or extrinsic decisions. Groups of objects will be equally definite to all persons, but groups of groups will be recognizable only if their definitions are unambiguous.

For example, the words that have been assembled into this sentence form a group that is entirely definite. Any person can recognize the group of words and its limits. On the other hand, if one suggests two groups of dogs, the large dogs and the small dogs, no one will be certain where to draw the line between the two. The former group(the sentence) is objective as a group; the latter ones are subjective, simply because of the indefinite nature of the distinctions.

The taxonomic groups, then, exist and can be objective. We can describe them, combine them, subdivide them. In classification several kinds are assembled to form a group, and several such groups into a more inclusive group. Then several of these more-inclusive-groups are assembled into a still-more-inclusive-group.

Chart

This figure indicates that kind K, for example, belongs to group 3, to more-inclusive group b, and to still-more-inclusive group 1. There are four levels in these groupings, and the levels are called "categories". In this arbitrary case the categories are kind, group, more-inclusive-group, and still-more-inclusive-group. This ascending scale is a "hierarchy", which is a series of levels or categories into which the groups can be arranged.

In zoological classification, the levels in the hierarchy are named species, genus, family, order, class, phylum, and kingdom, from the least inclusive to the most inclusive. Some of these are shown in this diagram.

It's not correct to speak of some categories as larger than others, because a phylum might consist of a single species and thus be no larger. The categories are properly described as higher and lower. The groups assigned to the categories, however, are not really higher or lower; they are simply more or less inclusive, or can even be described as larger or smaller, because they are at least potentially so. The place of the category in the hierarchy is definite; the group may or may not be definite, and the placing of it in that category is entirely definite and unequivocal.

You are all familiar with the customary hierarchy, of which this list is one of the most expanded forms. There may even be additional

levels or categories inserted among these, and I know of no group of animals that uses all of these.(Mammal example) (Incidentally, there are no such things as obligatory categories; any of these may be omitted, if the small number of species makes this reasonable.) For instance, the phylum Phoronida contains just one genus. Why waste time listing a class, a subclass, an order, and a family?

What it is that is grouped at each level in the hierarchy is not strictly free of opinion. Here is my preference of how we can look at each level.

In order to use the categories there must be a name for each one, and it's accepted procedure to call them species, genus, family, and so on. But these names are also applied to the groups placed in the levels. A group placed in the family level is called a family. This leads readily to misunderstanding when it's not clear whether the word "family" refers to a particular family group or to the level at which such family groups are placed.

There can be no definition of what a family is, or what a superclass is. It's either a level in the hierarchy, defined solely by its positionin the series, or it's a group(taxon) placed at the family or superclass level and called a family or a superclass. The only standard to determine the correct level for a group is the agreement of specialists. The group may be quite definite and understood by all, as most taxa are, but its level or category may be subject to much difference of opinion. It may appear in various classifications as a class, a subclass, an order, or even a phylim, according to the views of the particular classifier. (We'll see examples of this later on).

This is almost the only place where we can legitimately talk of subjectivity. It pained me the other day to hear Dr. Amadon state that the species are objective but that both higher and lower taxa are subjective. We must admit the subjectivity of subspecies because that's how taxa at that level are defined, as partially distinct. But there's nothing whatever subjective about the groups at any higher level. L have no hesitation in making this drastic statement, although I'm sure it comes as a shock to some of you. Here's why.

The word group implies the objects specified. The group contains the objects specified and excludes all those not specified. The group is thus completely objective, what Simpson calls non-arbitrary. When I say Nematoda, I mean the group of animals for which I use that name, and the group is objective. You may not know exactly what my group includes, until I list them, but there is no subjectivity.

The minute we specify that this group(or taxon) is a phylum, then we are starting at opinion, and this is subjective. It's the level in the hierarchy at which any group should be placed that brings in the subjectivity. It's impossible to prove that any particular group(or taxon) BELONGS to any particular level(or category). The groups of animals, at any level, if they really are groups, are entirely free of subjectivity, by definition.

The subjectivity of the assignment of the groups into the categories is so great that it has produced this misunderstanding.

Thus we have: CONCEPT, the idea produced in the mind of an individual by sense impressions and imagination, known only through statements about

it; GROUP, the limited set of objects or sets segregated on any basis by any individual; CATEGORY, one of the levels in the hierarchy, to which the groups may be assigned; SPECIES, (1) one of the groups, the one placed in the category called the species level(a species group); and (2) the category or level at which the species groups are placed (the species level).

It's very common, even among taxonomists, to use the word "category" when "group" is intended, and to mix these two taxonomic meanings of the word "species".

(Gregg diagram)

This diagram is from Gregg, who is not a taxonomist but who dabbled very effectively in the language of taxonomy.

There are a few taxonomists who have clearly distinguished between the categories and groups as used in zoological classification. One is Simpson in 1945, who makes the distinction explicitly and then uses the words in their proper meaning. He states: "The framework of classification is to equate...groups of animals with the categories of the hierarchy...." Also: "All categories above the species have in common that they may include groups discontinuous...between themselves." The categories include groups. Although he does not directly discuss the distinction between categories and groups, it's clear that the categorical hierarchy is an arbitrary arrangement and that the groups, as natural as they can be made, are assigned to the categories by the taxonomists.

Things are not classified into categories but into groups. It makes no difference what things are being classified. When a taxonomist sets out to classify groups, he does not classify them into categories either but into more-inclusive groups. Only when he has groups, more-inclusive groups, and still-more-inclusive groups can he make use of the hierarchical levels which are called categories. He does this by assigning each group to some level, the more inclusive groups to the higher levels. It also makes no difference what basis he uses for the grouping-- the hierarchical system is not dependent upon the nature of the groups.

To recapitulate:

The groups of animals are taxa. Each taxon is placed in some level of the hierarchy. This level is the category. A category can be higher or lower than some other one, so we may speak of a higher category. The taxa are not higher or lower but are placed in higher or lower categories(levels or ranks). The taxa are more- or less-inclusive (include more or fewer subgroups or species.)

The categories have names, but these are terms and not names in zoological nomenclature. (They are kingdom, phylum, class, and so on.) The taxa also have names--the zoological anmes.

It's an error to state, "This animal belongs in the category Mammalia." Mammalia is the name of a taxon, not of a category. To refer to "the origin of higher categories" is not taxonomically meaningful, because it's the taxa which are studied in this regard; the categories originate only in man's mind.

It's necessary to make a careful distinction between names, taxa, and categories both in taxonomic work and in nomenclature. The extra word or two required to do this in each case is well rewarded in clarity of

thinking and understanding.

The data of taxonomy

The things that can be known about kinds and groups of animals are the potential data of taxonomy. Taxonomy and classification have always been overwhelmingly structural in their data, primarily because these were the only data consistently available. Classification serves to store all kinds of data if these are associated with known species or other taxa.

Some writers have recently stated that taxonomy cannot be adequate if it uses only anatomical or structural data(usually called morphological), but this involves at least two important misconceptions. First, it is implied that other types of data are largely available. But it's probable that there is no genus of animals of any size about which there is enough non-structural data for classification of the species to be accomplished by its use alone. The genus Drosophila may be an exception, but there seem to be, even in this much-worked group, some species which are known only from structural features. Even if such exceptions were fairly numerous, the great bulk of animal species cannot at the present time be compared on the basis of any data other than those obtainable from preserved specimens. Second, it is implied that use of non-structural data is a recent development that has been neglected by taxonomists. The fact is that non-structural data have been used since the time of Linnaeus in increasing amounts as such data have become available. But, because such non-structural data are not even now ordinarily available in sufficient completeness, these data are, and can be, used only in rare cases to solve problems that have proved puzzling. Furthermore, in most cases where such data are available and are studied, they merely corroborate the conclusions from structural data.

There has been no great change in the practice of taxonomy in recent years, im spite of some statements to the contrary. There's no prospect of change in the future and no reason why one should expect it. The present system is almost infinitely expandable, and there are many groups in which structural data will continue to be adequate.

Animals are still classified almost entirely on the basis of comparison of their attributes. Whereas a few score years ago the data generally available for this comparison were largely structural, today taxonomists frequently know something also of the physiology, ecology, distribution, and even biochemistry of some of the animals studied, but seldom do they have enough of these data for general use.

The newer types of data or methods or study have sometimes been presented as if they were panaceas for all difficulties in taxonomy. They have not proved to be any such thing. There's no reason to believe that these newer features are any less subject to the difficulties that beset the use of the older data--such as irregular variability, convergence, parallelism, difficulty of observation, and so on. There's no reason to believe that they are as a group any more surely related to the basic nature of the species or the hereditary processes. All characters are correlated to some extent in the gene complement. Some are controlled directly and absolutely by the genes; some are merely initiated or limited by the genes. It doesn't appear that any one type is more reliable than the others.

The attributes of animals, when recorded in terms that are at

least potentially comparative, form the data about kinds. Although the data available in Linnaeus' time were almost exclusively the physical features of the specimens, after two hundred years of zoological study there is available now a large range of attributes, including much beside the physical structure. As it is sometimes misunderstood how wide a variety is represented in this range of attributes, we might suggest a few of them.

At a symposium at Denver a few years ago we had twelve speakers describing twelve widely different sorts of data that could be used in classification, from crystal structure of hardparts to behavior, parasites, and ecological reactions. They can be at all levels from true morphology (form, symmetry, arrangement, polymorphism), to gross structures, to tissues, to cells, and to molecules. From populations to individuals or to colonies.

Anything that can be compared is potentially taxonomic data. Although the taxonomist MAY use these data in classifying the animals--and he certainly will use some of them--the rest of the data will NOT be useful to him for a variety of reasons, such as: (1) the data are incomplete, being available only for a part of the specimens, species, or groups being classified; (2) the data are difficult to present, as may be the case with complex three-dimensional shapes; (3) the data may be so numerous that they are hard to interpret, even when tabulated, as is the case with much of the numerical data used in computer analysis; (4) the data in question may be fully correlated with some other type of data that is easier to handle, as is the case with much genetic data which directly produce visible features that are more readily compared; or (5) the data may be produced by procedures normally beyond the facilities of the taxonomist, who thus has difficulty in repeating, verifying, and adding to the results, as is frequently the case with serological and electrophoretic data.

Whatever type of data is used, they must at the outset be interpreted or adapted for this particular purpose. The taxonomist must select the specific items he will use, the particular forms of these that will be compared--in the modern phrase, the parameters of the classification he's producing. These individual features to be employed are the taxonomic characters.

Taxonomic characters

Some recent books have used the term "character" in much the same general meaning that I just used for "data". For example, Davis & Heywood write: "Taxonomic evidence(in other words, characters) can be drawn from any part and phase of development...." They equate characters with taxonomic evidence. They define a character for practical purposes as: "any feature whose expression can be measured, counted or otherwise assessed...." The character is the feature, not its expression.

This is a reasonable usage and one consistently followed in that book. It requires that each character be, in their words, "divisible into two or more expressions or states(including presence or absence in qualitative characters)." For example, a character might be the number of segments in the tarsus of a beetle. It can be expressed in different beetles as 1, 2, 3, 4, or 5 segments. Or it might be a certain spot of red on the wing of a bird, expressed as presence or absence.

This usage does not conform to the common usage of "character" in zoological taxonomy. For example, Mayr, Linsley, and Usinger remark that

"It must be determined how constant a given character is." In the system of Davis and Heywood, one couldn't use a constant character but would want to know how constant is each expression of the character. Again in Mayr, Linsley, and Usinger, "taxonomic characters should not be drawn from single representatives of populations...." Only one expression of the character could be so drawn, if we were using the Davis and Heywood system.

There seems to be no reason to abandon the customary taxonomic definition of the word "character", which provides a clearer distinction from the general term "taxonomic data." We would then apply the word "character" to the expression of the feature in the individual. We would not say that a certain seta is a character but the absence of that seta is a different character. This seems to be more in keeping with the common practice of saying that the character which separates species A from all other species is the presence of a certain feature.

In several recent works Simpson uses the phrase "characters in common" when speaking of the similarities between two groups. If he were using the dual-type character, it would have served to show the dissimilarities between groups, but to show similarities or characters in common, one must be using "character" as a single expression.

This distinction really reflects no fundamental difference in classification or philosophy. It must be understood, however, which of these two meanings is intended, whenever the word "character" is encountered. The system of Davis and Heywood is also used by the numerical taxonomists, because of the nature of their computers.

Thus, characters are the features of the individual animals. Taxonomic characters are the ones chosen by the taxonomist for use in discrimination or grouping.

This enables us to speak of; diagnostic characters, key characters, and qualitative or quantitative characters. Time won't permit me to go into the arguments of the numerical taxonomists that quantitative characters are better than qualitative. The arguments are cogent only insofar as you have a computer that can digest only such numbers.

It is not appropriate to urge all taxonomists to use numerical characters exclusively. In some situations quantitatively expressed characters can be more definite and more easily compared. The taxonomist should be alert to recognize these situations. He should be equally alert to use verbal characterizations when appropriate and graphic characterizations when appropriate. He should not feel that there is any inherent difference in the various ways of expressing his observations. He will, however, find it advisable to make his records comparable to those of other workers in his field. If they are not, he will very likely find his work unused and unaccepted. This actually happened to Adanson more than a century ago, when he urged a radically new method of classification which could not readily be incorporated into the ways of his time.

Methods of classification

There are few subjects in systematics so difficult to write or talk about as the actual procedures employed in classifying or reclassifying a groups of animals. As a result, almost nothing has been written on the subject. Even the most recent book on taxonomy, before mine, and

that's Simpson 1961, which deals with many philosophical aspects of classification, has little to say on the actual methods of classifying. It's evident from published classifications that there are no well-known procedures in use in all groups of animals. It seems extremely likely that clear-cut concepts and procedures do NOT have any significant influence on classifiers in general.

Classification in the technical sense consists of five avtivities, as shown in your outline: The objects are grouped (1) and the groups must be distinct(2). A hierarchy of levels must be chosen (3) or the customary one accepted, and the groups assigned to the levels (4). Finally names must be applied to the groups (5).

It must not be assumed, however, that classification usually starts out with ungrouped objects, no hierarchy, and no names. This happens so rarely after two hundred years of classifying animals that we can dismiss it as not occurring at all. Classification always proceeds to build upon previous classification; there are always groups, levels, hierarchy, and names. Today, classification is largely the re-evaluation of earlier classifications with addition of new species, new groups, new data, and new understandings.

Although there is almost always previous work to build upon, it's a mistake to think that classification of organisms is complete or nearly so. The remark of Davis and Heywood about plants, that 'the classification of a large part of the world's flora is still in its early or pioneer stages", applies equally to animals(fauna). The well-classified parts of the Animal Kingdom form no more than a hundredth part of the known fauna and probably only a thousandth part of what actually exists.

All this classification is comparative. It's possible to outline this comparing activity in general terms without referring to homology, but after last Wednesday's talk on functional morphology. I just had to go back to my room and add a pharagraph on homology to this talk. I can't allow it to stand that homology can be "based on" something which no one can use in determining whether there is homology. (I'm sure that Dr. Bock merely failed to get across to us the real basis of his position.)

Instead of arguing at length the differences between theoretical definitions and working definitions, I want to give you very simply a unified scheme which seems to make homology both useful and definable, and I'm happy that a later speaker has given me some support from a slightly different angle.

Somewhat to my surprise, I must confess, Dr. Sibley gave the clearest statement of what classification is of any of our speakers. He emphasized the comparative method. And he showed clearly that both differences and similarities are of real importance. It was implicit in his remarks, although not quite so much emphasized, that comparisons must be of corresponding features.

Here we have the essence of classification in a nutshell. We compare corresponding features of objects and groups of objects to see how they are similar(to form groups of them) and find how they are different (to separate the groups). The essential ideas are comparison, correspondence of features, and similarities and differences among these features.

This means that the taxonomic solution to the problem of homology is to treat as homologous those features that correspond, that are

comparable. And although Dr. Bock seemed to deny this directly, this DOES mean correspond in position, connection, structure, development, and so on.

There are two basic methods of classifying animals, or anything else, almost irrespective of your goal in classifying. Both of these have been used in zoology, but one necessarily preceded the other in history.

First, the method of association. Historically, when the first taxonomists sat down to classify, they had before them what was actually, as well as in our perspective, a small number of specimens of a small number of kinds. In studying these specimens they found that some of them had many features in common and some only a few. Knowledge of these animals was adequate to show that some ressembled each other about as much as the members of one brood, or the offspring of one pair of parents. These were assembled into a group called a species. It was believed that these were the individuals which could reproduce their own kind, with reappearance of the same minor features indefinitely in various combinations. It took no great effort to assemble all the available specimens into a very few thousand kind, or species. This activity was classification, at that time. It was, in fact, the only classification possible in the beginning.

It was then seen that certain of the species were so similar to each other in so many ways that it was possible, and useful, to bring these similar ones together in a group of species that was called a genus. Similarly, some of the genera were so much alike that they were grouped into orders. The orders were then grouped into classes. In all of this the essential feature was recognition that because of differential similarity, certain distinct entities could be brought together as a definable group made up of several of the lesser groups. The arrangement of the groups into the more inclusive super-groups in the hierarchy of ascending levels was a device well known in logic long before zoological taxonomy became a formal study. Grouping of a comparatively few objects or groups of objects thus started the system.

Once such a system was started, in the formal sense by Linnaeus in the mid-eighteenth century, new discoveries were simply inserted into the existing groups at most levels. If they differed from all known species in ways believed to be outside the realm of filial diversity, they were segregated into new species.

This process did not really involve much classification. It's still a very common procedure, often denoted by the expression "descriptive taxonomy".

As the number of species increased and were assigned to the known genera, these genera came to contain species more and more diverse. Finally, students divided the genera by recognizing that the included species could be grouped into two or more clear-cut groups that could themselves be called genera. The same thing happened to orders and classes, so that the number of groups increased at all levels. As more and more specimens were collected in all parts of the world. many were at once seen to be so different from all known species that they couldn't be put in any known genus. At the time these new species were described, they were grouped apart in new genera, and even in new orders and classes. All of this involved primarily recognition, first, of groups of specimens as probably being within the range of variation of a single kind; second, of groups of these kinds or species under the term "genus", and third,

of groups of these groups as orders and classes. Grouping predominated all this activity, and characters held in common were the basis of the grouping.

Second, the.method.of.subdivision. When a large number of species had become known, and they had been grouped into genera, orders, and classes, it was possible for taxonomists to use a different approach. When a sufficient number of specimens in one order were available for study, representing a major part of the known species, the taxonomist could disregard all previous classification, and even identification, and work by subdividing groups instead of grouping them. For this purpose, he would, in effect, start by treating all the specimens as comprising one group, an order perhaps. Examination of these specimens would immediately reveal that they differed from each other in various ways. The taxonomist, being familiar with these animals, knew much about the variety that occurred among these specimens. He could, usually without any difficulty, divide the specimens into two lots on the basis of features that seemed to him to be the least likely to be the result of close common heredity, environment, or the diversity usually associated with species or genera. Each of these segregated groups could again be subdivided, until finally all the known specimens were distributed into genera and then into species on the basis of the extent and manner in which they were different.

It was, of course, found necessary to insert additional levels into the system, families, suborders, and many others. At each level the goal was to have a comparitively homogenous group--a genus containing only species very much alike, and a family containing only species more like each other than like those in other families. Groups were divided and subdivided whenever appropriate features provided a distinction. In this way, subdivision was the keynote, although of course grouping was also involved.

This method of subdivision is quite often the principal approach in a monograph, where a reclassification is undertaken. Previous groupings may be temporarily or even permanently discarded, while the actual specimens are being sorted by subdivision of the entire lot into sublots.

When a group has been well classified previously, such reclassification by subdivision will probably end up with much the same grouping as before. If the previous classification has been based on poor work and faulty decisions, the new one may be substantially different. The princioal advantage of subdivision over association is that you can readily abandon faulty work of the past. In the usual classification by association it is quite difficult to correct major faulty previous work. Nevertheless, classification by association is the overwhelming choice, partly because it is what we see other people doing.

In Summary.

Classification is a highly practical activity that organizes things or ideas. Science may be defined as organized knowledge, and classification is the principal form of organization in biology. This activity may also be appropriately termed 'systematizing', the production of a system of knowledge arranged to facilitate the use of that knowledge.

The process of classifying thus stores the knowledge. This is its chief practical purpose. The act of classifying produces new knowledge about the groups. This new knowledge is also stored and is often more

useful than the original knowledge on which the system was built.

It's possible to classify because the immense diversity of organisms is not a continuous sequence of minute differences but a series of discrete groups, even though our ideas of evolution might lead us to expect a continuum. Gaps in the diversity do exist and make possible the definition of the groups. A variety of aspects could be used for the grouping, but the necessity in zoology to work at times with preserved specimens has channelled the grouping on the basis of physical features of the body which can be preserved.

The actual classification can be done by grouping like things starting at the bottom, or it can be done by dividing the entire complex into groups and each of these into subgroups. These methods are both accomplished by comparison of corresponding features of the specimens or groups. They differ only in the direction of approach.

The difficulties in classification are those of understanding the nature of the animals. The data are very largely objective. The selection of the data to be employed is entirely subjective. Onyl detailed comparative knowledge of the animals, of the methods of classification, and of the past studies on these animals will produce effective classifications.

HISTORY, PHILOSOPHY, AND DEVELOPMENT OF NOMENCLATURE

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It seems to me nomenclature is an essential thing in taxonomic work. As Needham of Cornell once said, the "names are the handles by means of which we move all our intellectual luggage". And on page 373 of Blackwelder's book you'll find an appropriate quotation from Ferris' book on the Principles of Systematic Entomology. We cannot dispense with names. They are an essential part of the equipment with which we must work. Anyone who proposes to be called a systematist must consider it a part of his equipment for his profession to know something of the commonly accepted rules and procedures that govern the application of names. Certainly we need some system, some definition, some precision to handle the tremendous number of names, to get some system, some order, to avoid chaos in talking about the multitutde of organisms. This is more critical in some groups than in others, of course.

Now this doesn't mean that all of you have to be nomenclaturists. I'm sure most of you won't be. As my friend, Herbert Friedmann the ornithologist once said, "I view nomenclature like civil sanitation. I'm thoroughly in favor of it, but I don't want to do any of it myself". We still have to know something about the rules and the handling of names. We deal with names. We communicate with others about them. We record data about organisms in terms of their names. True. We could use numbers. We could use formulae, or we could use something else. Possibly, as numerical taxonomists would insist, we should use something else, but nevertheless we use names. In the forseeable future, I think we're going to use names.

Now what I propose to do this morning is to talk first about the history of nomenclature. I'll follow roughly the order in your outline. I'll talk rather quickly about the history of nomenclature, because this is pretty much factual. I don't know that there will be any particular questions or discussion. I don't mean to shut it off if you have any, but it's not what I want to emphasize. I want to get on to the code. I think that's the part that we're most interested in, the place where there are the most problems and some controversies.

I want to review, to give us the background, however, because our roots are in the past. The roots of the code are in the past. I want to get on rather quickly to the philosophy of nomenclature and I'm going to generalize so much that here again we may be able to save some time by a relatively short discussion, but that's entirely up to you. And then on to the code of nomenclature.

Now for the history. The early codes, quite naturally, were pretty much the result of individuals. And as you might expect, some of the early codes were those of Linnaeus. His first code, I believe his first, the Critica Botanica appeared in 1737, and his Philosophia Botanica in 1751. They appear from their titles to be botanical, but Linnaeus was both a botanist and a zoologist, as you know, or can be called that in modern terms. Perhaps he was a naturalist then. And his codes really applied to both botany and zoology. At least after the mid-nineteenth century, and probably long before, botany and zoology went their own

ways, and actually what I speak about here, refers to zoology alone.

There were other personal codes of the time. I mention in passing that of Fabricius, 1778, called Philosophia Entomologica. I would note that even in that early time, there were people thinking in terms of entomological nomenclature, rather than zoological nomenclature. This was probably natural because the impact of the large number of species hit entomological taxonomy a little earlier than it hit some other branches of zoology. Their problems became greater. The obvious need for some rules, some procedures was perhaps more evident in entomology. But this has continued all the way through, even to the present time.

Now these early codes of Linnaeus and so on were successful up to a point, as long as taxonomy was small, but the increase in the number of species very soon led to greater and greater conflicts between names, duplications of names, different procedures for handling things, arguments among taxonomists; so in the early 1840's the British Association for the Advancement of Science took the lead in appointing a committee to draw up a set of canons or rules for zoological nomenclature. This is often referred to as the British Association Code also the Stricklandian Code, after Hugh Strickland, the recorder or secretary of the committee. This was printed in 1842. It was an excellent code. It was very well thought out. Maybe it was a good code because it wasn't created by a colloquium, but by a small committee that could really work on the details of a code and the interaction of rules. I think it is safe to say that it is the basis of almost all of the later codes of nomenclature.

Just as an interesting sidelight, one of the members of this committee was Mr. Charles Darwin. I'm sure a great many evolutionists of the present time wouldn't be caught dead on a committee of nomenclature. But Darwin's name appears there. I've often wondered just how much he actually contributed to the deliberations of this committee. I've never gone back to Darwin's letters to see whether there is any reference to this or not. It might be interesting to do that sometime.

In the next 50 years or so, there was great effort expended on the rules of nomenclature. For example the congress of Entomologists at Dresden in 1858 adopted a set of so-called laws for nomenclautre.

The Stricklandian Code went through a series of editions. In 1877, the AAAS published a code or report prepared by W. H. Dale, which had great influence. In the same year, the entomological club of the AAAS, the ancestor of the present national entomological society, published a short 3-page set of rules. Again entomologists were prominent.

On to 1881, the Zoological Society of France adopted a code of nomenclature. About the same time the Second International Congress of Geology in Bologna, Italy, adopted its own code. It was based on the Stricklandian Code, but it had some differences. It's usually referred to as the Douville Code after the Secretary. The American Ornithological Union developed its famous A. O. U. code in connection with the A. O. U. Check List of North American birds in 1886. This has had several editions, also, but that was the original one. All of these were national or individual codes. They had influence, but there were still no international codes.

In 1889 the first international Congress of Zoology was meeting in Paris, and the Zoological Society of France, led by Professor Rapheal

Blanchard, took the initiative and proposed an international code of nomenclature. This was not the first code, remember. That was a proposal by the Zoological Society of France, and circulated to other societies and organizations for their comment. I believe this 1889 proposal was actually adopted by the Paris Congress and again by the 2nd Congress of Moscow in 1892, but it was adopted as a working document rather than as a formal code.

During this time, at the end of the century, there were many of these codes in effect, and followed by different groups--the AOU code in America and other places, the Stricklandian code still mainly adhered to in England, and the German Zoological Society had adopted its own code in the meantime, perhaps for nationalistic reasons. There was this Blanchard code, adopted by the Zoological Society of France, and so on.

But efforts continued towards an international code. Our own Charles Wardell Stiles was active throughout this period. We went through a series of zoological congresses. There were various parliamentary maneuverings, discussions of disputed points, and compromises achieved, some things not covered because they couldn't agree. But finally an international code was adopted at the Zoological Congress in Berlin in 1901. A committee of three, Blanchard of France Stiles of the United States, and von Maehrenthal of Berlin, was appointed to prepare the French, English and German versions of the international code. In case of difference between these codes, the French text was the definitive one. This had led to the citation of this international code as the Regles. I would prefer, and I will say in this talk, Rules, but you will understand what I am talking about.

For one reason or other, the preparation of this code was rather delayed, and it was not ready until the next Congress in 1904. But it was officially adopted at that congress and finally published in 1905. I might mention at this point that I have on the table here for your later reexamination, a number of different codes and documents. Here for example, is a copy of the original code. There are others here in a bound volume, the Stricklandian Code, and some of the early ones as well as some of the later documents. The Biological Society of Washington frequently reprinted the code. This was one of the most readily available copies of the code in English. Interestingly enough, when I went to Copenhagen, I found Secretary Hemming using this one also as his English copy of the Code. I also have copies of the Botanical Code, and of the code for Bacteria and Viruses, some of the other official lists and indexes, the Copenhagen Decisions, and other things that may be referred to from time to time.

This first international code published in 1905 lasted until the new code, published in 1961. There were a few amendments along the way. There were several congresses which worked on it, as I will come to, but actually there have been only two international codes for zoological nomenclature.

Through the years, the International Commission on Zoological Nomenclature issued a number of opinions. They built up a set of case law. Some regarded these as Opinions with a capital O, like those of the Supreme Court. Others regarded them as opinions with a small o, simply the expressions of a group of people; you could pay any attention to them or disregard them, as you wished. Because of this uncertainty because of differing of opinions, because of inadequacies in the old code, and some newer things coming along neotypes, for example, the

time was certainly over-ripe for a comprehensive revision.

This was begun at the International Congress of Zoology at Paris in 1948. That set off a long period of bitterness and dispute. There are at least three people here, Blackwelder, Usinger, and myself, who fought this thing through from the very beginning. I think we can say, paraphrasing the famous statement in history, that all of this we saw and much of this we were. I believe Dr. Wetmore was involved in some of it. However, I think the three of us have been at more of the congresses, more directly involved.

This revision undertaken at the congress in Paris sparked an era of ill feeling. It was unannounced to zoologists as a whole, and even the commissioners did not realize what was going to happen. And as a result, there were publications, charges, and countercharges. The Nomenclature Discussion Group here at the Smithsonian led the fight almost alone, I'm sorry to say. If we had had more support we might have had more effect at a time when it might have saved us a great deal of subsequent difficulty. But there was always the feeling let's not rock the boat, let's not disturb what we have gained in international nomenclature, and so the thing went on.

As a result of the Paris Congress, we were supposed to have a code of nomenclature prepared by jurists. Most of us shuddered at that term. As a matter of fact, such a code never appeared, perhaps partly as a result of the protests of the Washington group, perhaps partly as a result of realization by some people of common sense that this jurist code simply wouldn't be accepted by zoologists.

A Colloquium on Nomenclature was organized for one week preceding the Congress of Zoology at Copenhagen in 1953. I don't know that anyone there actually saw this jurist code. Someone who saw it in England told me that it was a manuscript (about so high), and it must have been terrifically complicated legalistic language. I doubt very much that they even brought it to Copenhagen. At least I don't know anyone who saw it there.

This was announced beforehand. A relatively small, very interested group of perhaps 30 or 40 people met for one week preceding the Congress in long sessions every day, thrashing out a number of these details under the chairmanship of Secretary Hemming. We took decisions on a number of items, but still we didn't cover everything. So as a result of that, Professor J. Chester Bradly of Cornell, who by this time was President of the Commission, was charged with preparing a draft of the new code of nomenclature to bring to the next congress. So he had the job of putting together the Copenhagen decisions on nomenclature (which were later published in this thin but very wordy volume), the old code, the Paris decisions (such as were covered or reversed), the Opinions, the relevant decisions and substance in the Opinions--all of this he had the job of bringing together in a draft of the code. This he did and this was ready for the London Congress in 1958. This Bradley Code was a very well worked out code, very well rounded. The language is not florid, not excessively wordy. It is in an old-fashioned prose in some ways, with more words than most of us would like to use, but it was a very well worked out, very thoughtful, well integrated code. There were a number of places where he could not decide what to do, and he presented alternatives, and added discussions. This increased the size, of course. It was a working document, but without it our task would have been, I think, hopeless.

Another Colloquium was arranged for a week preceding the London Congress. The Bradley Draft was finally published about 6 months preceding the Congress. There was immediately a flood of comment. They undertook to publish all these comments, and those of us who were going to the Congress and to the Colloquium had to study the code and all the comments, and most of this was handed to us when we arrived at the Congress.

We met for a week at London doing the best we could with these things. Every morning we had on our desks a mimeographed list of what had happened the day before, and I tried to proof-read that. In addition to trying to digest and keep track of all the discussions, I was appointed chairman of a coordinating committee to try and put this together as we went along, and I worked on that almost every evening, and during the congress, getting some kind of a code ready for final presentation to the Section on Nomenclature. I worked on that day and night. I heard not a single paper at the entire Congress of Zoology. I took time off only for the main reception at the British Museum and a reception for visiting entomologists at the Entomological Society of London.

This committee produced a code of a sort that could be presented to the Section on Nomenclature. The editorial committee did quite a careful job of honing the first few articles, but the rest of it finally ended up simply as a cut and paste job. We took the Bradley Draft, cut it apart, eliminated the lines, or paragraphs, or what-not that had been changed or deleted by the Colloquium, and put it together, and this was mimeographed and presented to the Section. It was adopted, and the preparation of the final code was entrusted to an editorial committee for the completion of the code, two English, two French, and two Americans, of which Dr. Norman Stoll, parasitologist of the Rockefeller Institute and myself were the Americans. The other members were N. D. Riley, an entomologist, and C. W. Wright paleontologist of London, and Forest, carcinologist, and Vayssiere, entomologist of Paris, (his place taken later by Dollfus, parasitologist. These six were assisted by R. V. Melville, paleontologist, the Assistant Secretary of the Commission. We worked for three years following the congress in '58; we met together in London in '59. I have a file drawer filled with correspondence, back and forth in the different languages. We would get something agreed upon, and Forest would put it into French. He would call our attention to the fact that it didn't fit the requirements of French grammar, or something pointed out a weakness, or something would not be clear expressed in French. Then we would change the English to make it work better, and then when the whole thing was agreed upon after endless letters, someone would come up with a change of a word, or the deletion of a comma, and it would throw the whole thing into question. You finally got that worked out, and agreed; you went on, and then weeks later someone would call attention to the fact that you didn't realize when you left out that comma, it threw something else off back in another article, and then you had to go back and fix it, and on and on and on.

This was not an easy task, by any means, I can assure you. And when the code was finally completed it went to the Commission. They had their comments, and we had to try and resolve those problems. It was finally approved, and after some more delays, it was finally published on November 6, 1961.

The Washington Congress came along in 1963 and made a very few changes. A second printing--I don't like to call it an edition, was published in 1964. Basically this is not really an edition but I guess

technically it is. Actually, they ran out of codes. They needed more for sale, so while they were reprinting it, they put into it the few changes that were made. They also made some improvements, such as putting the article numbers at the top of the page, for easier reference. At any rate, after all these years, we do have finally a second code of nomenclature for better or worse.

Through this period there have been some major controversies. I think I've listed them here in the mimeographed material. I'll refer to them very briefly. No need to spend any great amount of time but there have been numerous minor controversies.

As to the beginning date of priority, I think most of us don t even realize any more that there was any dispute about this. We have accepted 1758 for so long, it's a standard thing. We learned it in our beginning zoology. At one time however, there was considerable dispute. They believed it should start with the 12th edition, but this again is long passed by. We note in passing that the botanists use 1753 for the beginning date for most of their groups, but for some groups those not well understood in the early days, priority is based on several later dates, even as late as 1900 for one group. I think that perhaps zoologists might have been well advised to do this in certain groups, but we didn't.

The second controversy--binary vs binomial nomenclature: The old code (1905) said binary nomenclature, that is, there were basically two fundamental categories, the genus and the species. Binomial nomenclature said there must be one name for each of these, a name for a genus, and a name for a species, giving you a binomen. The old code permitted, then, the recognition of zoological works in that transition period, some of it post-Linnean, when authors were using a single name for the genus, but still had a polynomial expression for the species. It happens in entomology that a great many of some of our most familiar names, such as Stomoxys, or the stable fly, date from some of those works.

The Paris Congress came along and substituted the word binomial for binary. This of course, upset a lot of the older works in that transition period. This was, I think, a very unfortunate change. It was changing horses in the middle of a stream, and this always causes difficulty. Technically, if you had works in your group that involved some of these names and you didn't want to change them, they were widely used, important in economic fields, etc., you would have to apply to the Commission to save the work or save the generic names involved.

We considered this in our Washington Nomenclature Discussion Group, along with other disputed decisions of the Paris Congress. We were already protesting so many things so bitterly that this was one of the things we decided we could live with. We wanted to reduce our protests to a smaller number so as to have a greater impact. So we didn't protest it. I have thought since we should have.

A third controversy, page precedence vs the rule of the first reviser. Actually this controversy has persisted throughout the history of nomenclature. Of course, first revisers can always use page precedence as their first principle if they wish; there is nothing wrong with this. This has complicated the reaction of some people. It was first reviser in the old code; the Paris Congress changed to page precedence; a lot of people jumped in and made changes, some of them had been making changes on page precedence all the way along even though the old code said first

reviser. The Copenhagen Congress immediately promptly, and overwhelmingly changed back to first reviser. And that was confirmed at the London Congress.

Our fourth controversy deals with the classical vs the non-classical treatment of names. This is liable to be a continuing controversy, I'm afraid. It will never be entirely satisfactory. The old code, of course, and old times in general, were firmly on the side of classical treatment of names. Americans especially went to the original spelling thinking that they were following the international code. And how wrong they were. For example, you probably know the reptile genus Agkistrodon, the mocassins and copperheads, Agkistrodon mokasen, for example. The original spelling was Agkistrodon, 1799 and the spelling Ancistrodon, more correct transliteration, came along in 1830. Just to check up on these dates, I went back to Neaves, Nomenclature the other day and much to my astonishment, I found in Neave the entry Agkishodon, page 370 (as Agkistrodon, page 381). I don't know whether anybody has ever noticed this or not. Maybe it raises a question. Was there ever a first reviser? Maybe there never has been because there are two spellings in the original publication.

The point is Americans thought they were following the International Code. They used the English text of the Code and the English text said in the famous article 19 that the original spelling of a name is to be preserved unless an error of transcription or lapsus calami or typographical error is evident. The lapsus calami and typographical errors are irrelevant to my point here. But note that error in transcription.

Several years ago, Dr. Blackwelder, J. Brookes Knight, paleontologist, now dead, and myself worked on the general problem of errors and emendations of zoological names, and we produced what I have always thought was the best set of rules that have ever been produced. We argued and argued and argued for weeks about that thing. We would argue, then go back and think about it, then argue again. Points would be brought up, with the advantage that we worked in different fields. Things would come up, like names such as 4-maculatus. Brookes said, "Well, they're not valid, they're not Latin or latinized. 4-maculatus! Who ever heard of such a thing?" All we had to do was to open Linnaeus and show him many such names for insects. I'm sure that Linnaeus could write quadrimaculatus just as well as anybody else, but that was a short hand way of writing it and we still use it for insect labels where one does not wish to write out a long name such as quinquelineatus or something like that.

Well, this was the situation. Blackwelder, Knight, and Sabrosky worked out a plan very carefully, and then one of us had the idea, let's put this into French (the language of the definitive text) and see if it brings out any difficulties in our wording in English. Dr. Knight knew a French girl working there in paleontology at the time; and he had her put this thing into French. To our astonishment it turned out that the French word for transliteration was transcription. The English version of the Code was defective in taking a French word "transcription" and putting it into the English version as "transcription". Then the Americans became accustomed to thinking of that as just an error of copying.

Some years ago Dr. Usinger had an example, a collection in Cuba sealed in an insect drawer with dirty glass over it that wouldn't permit it

to be opened, so the labels had to read through the glass. Somebody read a label and wrote it down as a certain name. Later when they could actually get into the collection they found out that in their copying an error had been made and that it was a different name actually. This is an error of transcription to most Americans.

So you see what happened. The Americans thought they were following the code. Following "the original spelling is to be preserved" because there was no error of transcription in Agkistrodon and similar names. Actually we were violating the code all this time, when we thought so proudly that we were following it. The old code actually said that the original spelling of a name is to be preserved, unless an error of transliteration was evident, and then you corrected it. So this has led all these years to the Americans going back to the original spelling in the case of these incorrectly transliterated names, the rest of the world, in many cases, not following that. This has led to a terrific amount of difference of opinion.

Now at the London Congress this was considered. Prof. Bradley had a long appendix on the proper way to form names, and there is no objection to this. You do the best you can. But once you have incorrectly formed them, the London Congress said, then no matter how atrocious the bit of bastardy you have committed, it will remain as a monument to its author. And then they specifically said that errors of transliteration are not to be considered inadvertent errors, and therefore not to be corrected. And they made that retroactive to 1758 by a definite decision. This was not editorial committee.

This is a controversy that may continue. This again is a matter of changing horses in the middle of the stream. And it's a situation which I am not at all proud of--what the Americans have done in past years.

Then the last major controversy that I mention is priority versus conservation, epitomized by the so-called "Fifty-year rule", article 23b in the new code. I'll postpone discussion on that until later. The controversy on that is burning extremely brightly at the present time.

I think that closes my discussion of the history of nomenclature. I don't want a major break right now. I'll go on right into philosophy, but perhaps a few moments if you have any questions or comments.

VOICE: Has there been a controversial point having French and English equally efficient? It seems like many of these points could be avoided.

SPEAKER: The decision was definite to make the two texts both definitive texts. Maybe this isn't possible, I don't know. But at any rate it forced an effort to make the two texts exactly equivalent. We were very lucky to have in Jacques Forest of the Paris Museum, a very excellent and very careful worker in that respect. It has been questioned in one or two cases. I didn't think it was justified. I think actually the equivalence of the two texts is very good. You can't translate exactly word for word, of course, the languages don't permit that. But in its essence, I think the two languages are very close.

VOICE: Why these two languages? Why not some other languages?

SPEAKER: Part of this is tradition. The original ones were French,

English and German. German in the post-war period was unpopular. I'm not defending this. I'm just telling you this is it. Personally, I think the three texts should have been continued, but it would have made more difficulties. With just French and English you could have them on opposite pages and you can look from one to the other. This may be p particularly valuable for the many people in the world who do not have either French or English as their mother tongue. They may understand a little bit of both, and may be able to get the meaning this way. This can be very useful. There has been a lot of approbation for this. There have been, of course, texts in other languages. I was bringing so much that I didn't bring them along. For example, I have a couple of Spanish texts, one published in Madrid and the other published in Mexico City.

VOICE: Wouldn't you say that this reflects the fact that all the actual raw thinking and writing was either original in French or subsequent in English? This would have a great deal to do with it, wouldn't you say?

SPEAKER: This has been a great deal of it, of course. The domination of Prof. Blanchard--I should not domination--the leadership of Prof. Blanchard--this probably, in addition to the position of French language at the time, led to French as the defintive text.

VOICE: Are we developing into a time now with the dictionary writers giving us a bad time with our language where we're going to have to refer to a definitive dictionary also?

SPEAKER: No comment.

VOICE: The botanical code is also done in several languages. The English text is the official text, but it's done in French and German and one edition of the code has Spanish also.

SPEAKER: Yes. I think we want to add here that all are in the same volume.

VOICE: Just one correction here. Our nomenclature begins in 1754 rather than 1753.

SPEAKER: Oh good. I thought it was 3. I've been misquoting it.

VOICE: Aren't some of these other foreign language codes sufficiently sanctioned by the international commission? Wasn't there a Russian code that met with the approval of the commission?

SPEAKER: Well, it's a little hard to say. That was done by a commissioner. I can say positively in the case of one or two of the latest codes that it was never formally approved by the International commission as such. Perhaps it was okayed--the preparation of it was okayed by the secretariat or something like that. And of course, it stands to reason that they should do a faithful job of translation of it. I myself believe that the commission should formally approve these. The argument has been that the commission can't possibly approve all of them--they don't know enough about it. Well, some where or other, there should be some check on that and it would be an advantage to have the formal approval.

Well, a little on the philosophy of nomenclature. I'm not a philosopher. The rules of nomenclature aren't natural laws. We don't

deal with physical features, chemical reactions that can be said to be controlled by natural laws. On most matters of nomenclature there is no inherent right or wrong.

In most cases it would be very difficult to demonstrate that one method was better than another. You might, by a great deal of work, demonstrate that it would save you a little more time; but it's hard, and opinions change from one generation to the next. Think of what miniskirts would have done in Victorian England for example. But there have been changes, in general for the better. I think rules of nomenclature, like politics, can be defined as the art of the possible. They are what a given group of people can agree upon at a given time, and of course you can criticize a group of people as being unrepresentative, etc., but this is actually what it is. It's not necessarily the best rule, it's what can be agreed upon. It's not always possible to say what is the best rule, either. The early codes, however, in many cases were tributes to the astuteness or the far-sightedness of certain individuals or small groups of individuals, rather than what I might call legislative codes, such as those in the colloquia in recent times. Now, legislative codes may seem to be the democratic way to do things but there is not necessarily any merit in a consensus of the uninformed.

However, I have remarked that codes are not natural laws. Unfortunately for stability and universality, they are not laws of any kind. There is no enforcement, there are no penalties. In the long run, those that have merit will prevail and in the long run public opinion probably will trend in a certain direction and prevail, and only an occasional eccentric or egocentric individual will insist on going his own way. But I think perhaps zoological nomenclature could use a lot more discipline in the discipline. I think we could also use much more representative government or control of nomenclature. I think the botanists are very far ahead of us in that respect. Some of you might be interested in looking into the botanical arrangements.

Certainly non taxonomists must be horrified very often at the seemingly endless disputes and lack of agreements and divergent usages and so on. But life isn't easy. Agreement in principle is not always easy to obtain; interpretation may differ; agreement isn't universal. The Rule isn't universally followed, and of course, there is no enforcement. So the problem of rules in nomenclature is more than just a factual problem; it's partly a diplomatic problem. Of course everyone has a breaking point, but I'm afraid too many taxonomists tend to break on relatively slight causes. No code would satisfy everyone. To paraphrase Abraham Lincoln's statement, you can't please all of the people all of the time.

I have long been convinced that we would be farther ahead if we all got together behind a second best rule, if indeed you could determine what was the best, rather than to go our own ways because of difference of opinion on what was the best rule. I think we would be farther ahead in stability and universality, but this is a very difficult thing to sell. Individual, scientific and academic freedoms are all very well, but let's not base our fights on peanuts. That doesn't win us any respect.

I have listed here in the outline some of the basic goals of nomenclature. Actually, I would reverse the order of the code. The order says stability, universality, and uniqueness. I would say that the object of the code is to assure that names are unique and distinct. In other words, to mean one thing to all people at all times in all languages. That's easy to say, but it's not very easy to achieve.

And the second basic goal that names must be universal. We used to say uniform; "stability and uniformity" was the familiar expression. Now we say universality. Names should be universal, but we don't want to impress the ideas of uniformity if it means in any way getting away from flexibility and the right of individuals' opinions as to what species should be recognized and so on. With regard to the third major goal, stability, like sin, is much the matter of definition or opinion. I'm afraid that all too often we speak of stability when we really don't mean that. Absolute stability would be a straight jacket classification, and we certainly want flexibility. I won't discuss this in detail; I don't think that is necessary.

Going on to basic principles. I've listed a number of them here, not in any particular order of importance, unfortunately, if indeed, I could decide for myself. The independence of other nomenclatures--This is routine. The language, Latin, latinized or treated as such. The hierarchism, Dr. Blackwelder discussed that in some detail yesterday. We pretty well agreed, we don't all use all the possible categories, but in general we are agreed now on a certain sequence of categories in the hierarchy. This wasn't always so. I've seen works that used family between genus and species. Of course, the old genera were practically orders and groups of families anyway, but we are pretty well agreed now on the sequence of categories.

Coordinancy between each of the family-, genus-, and species-groups. This coordinate business is a very important part of the handling of names respectively within the family-group, the genus group, and the species-group. There were some arguments about that, as Dr. Blackwelder well pointed out. I think that one of the more difficult things to comprehend, in the matter of coordinancy, is not the application of the same rules, such as on formation of names, and latinizing, etc., but on this idea that once you propose a name for any category in the group it's automatically available at all of the levels.

If you propose a new subfamily, for example, based on the genus X-us, technically those are also possible and will date in authorship for purposes of priority from your subfamily proposal. Now, if you erected a family later, whoever did that later also has some credit for raising it. He undoubtedly has his reasons and so on. Historically and bibliographically you have to take account of that, but from the standpoint of coordinancy this is the situation. Obviously the names are not of the same value exactly. Generic and subgeneric names are treated in different ways. Subgeneric names are a parenthetical expression. They don't control the gender of adjectival specific names, and they're not quite of the same value. This is a difficult thing to express in codes and I'm not sure that the present code is satisfactory in that respect.

Binominal nomenclature--I've already referred to the old argument on binary and binomial.

Typification--The taxa are defined by types and of course a great many rules are concerned with these types. The nomenclatural types are pure name bearers. They are the guide around which you group the things that belong in with that particular type. It's not necessarily typical, and it's not the central feature necessarily; it's a nomenclatural type.

Priority is said in the preamble to be the basic principle of the code of nomenclature and indeed it is. It permeates the whole thing. Whatever we deal with, the first reviser, the first subsequent type designation, and so on. Almost everything is in terms of "the first", the prior one to do something. There have been limitations on that of course. It has been modified to a certain extent. The grant of the plenary powers to the International Commission to suspend the rules in certain cases was an attempt to mollify some of the objectors to changes of names. It also permitted the Commission to cut through a Gordian knot in some of these very knotty problems in nomenclature where the thing gets so mixed up that the simplest thing to do is to slice it down the middle and make an arbitrary decision. There is also the limitation on the law of priority, as represented in Article 23 (b), the fifty year rule. I'll discuss that later, also.

You'll find in the mimeographed material, a section on why change names. I don't want to discuss that at all now, it seems pretty routine.

Several items on the future of nomenclature, now. Numerical taxonomy-- I believe that the crusaders in this field, if I may call them such, have changed some of their extreme positions. Numbers are not going to replace names, at least not in the forseeable future. And certainly we are not going to do it by 1970, the date that Paul Ehrlich envisioned as his Utopia. It seems to me that numbers loose individuality; they don't make for rapid recognition, when in a large set of numbers you are talking about large numbers of species. They're not distinctive, they're not a minemonic aid, and they have difficulties in proof-reading; for example, a slight error would pass unnoticed. You can remember a few characteristic numbers, but when you are dealing with hundreds of thousands of species, this is something else. I simply do not believe that numbers will ever replace names. This is not to say that I do not believe that computers and numerical taxonomy have a place. They may have to number species in order to carry on in their work; this is something else again. But for ordinary recording and communication, I do not believe that numbers are going to replace names.

Incidentally, a speaker in the symposium on the philosophical basis of systematics published in the December, 1961 Systematic Zoology, said this, "It behooves us to make our taxonomic system as logical as possible and as phyletically correct as possible before the system is stabilized by the inertia of millions of standard punched cards and Mini-cards and of megamiles of magnetic tapes." I shudder at these words at the fixity of classification dictated by the inertia of already prepared cards and tape. We must still have flexibility.

I am concerned also with Michener's idea of a mononomial nomenclature, published in Systematic Zoology. This has some slight technical advantages, but it seems to me a very disastrous approach. One of the common complaints of binomial nomenclature is that it doesn't reflect classification. There are some people who seem to want names to do everything for you; not only identify and recognize, but classify too. Well, at least binominal nomenclature does one thing--it is an essential first step in classification. It places a species in the next higher taxon, the genus, and then you're on your way to classification. You can take it from there into other steps in the classification; you can use that as a basis for prediction: prediction of hosts, probable habits, probable control, anything you like. But the mononomial system would

destroy that, it seems to me. You break them up, you destroy any recognition. Take an Exus albus name: he proposes to write it all as one word from now on, and not worry about any changes. If it goes into a feminine genus, it's still exusalbus, one species, you see. We have a lot of classifying to do in insects yet. Suppose you have a big genus Exus, and you break it up, and you put it into a number of different places, now whenever you come to a name in the literature exus(something), all one word, you don't know which genus it belongs to. The genus Exus no longer has any significance. Exus may be in fifty different places as you have broken this thing up. I think this is a very backward step, a disastrous approach.

Rapport with Botany--I'm strongly in favor of this on many counts. Botanical nomenclature is far ahead of us in many respects, far superior to zoological nomenclature. I admire a great deal of it and would agree with all of it. Possibly we could persuade them that our use is better in some respects. I would have no objections whatsoever to becoming closer, particularly in matters of terminology. And their system for governing or controlling the rules of nomenclature, changes in it, is an admirable one, I think. I hope that the future will bring us much closer together.

Revision of the zoological code--From comments already, it is clear to me that we have tested the present one thoroughly enough so that we should proceed to repair and improve it. It's not sufficient merely to attack it, we ought to be constructive, we ought to make some suggestions, make some constructive changes. Dr. Blackwelder on page 382 of his book, says that "it is unlikely that wide adherence can be attained by the Commission and others to a code that is forever changing." In the particular context in which he said that there is a lot of merit in his remark, because he refers particularly to the changing of horses-the changing back and forth in the sequence of the Rules. But changes in substance and changes that improve wordy terminology and so on are something else. They are very urgently needed in the present code.

I might call attention to the fact that the botanists don't hesitate to publish codes frequently. There have been, as far as modern codes are concerned, one after each Congress since 1950: '50, '54, '59, and '64. I believe these are the dates of the Congresses rather than the dates of publication of the codes. But at any rate, you can see the sequence. So I see no reason why zoologists should be so reluctant, as some of them are and were at the Washington Congress, to revising the old one. I see only one draw-back, and a lot of us have this thing in mind, that the zoology congresses have not been very representative. For example, at the Colloquium in London there were more people from London alone than from the entire Western Hemisphere. Now particularly with the domination of some groups by some directors, this can lead to a very skewed distribution of opinion. Some of the objections have stemmed back to the objections to Secretary Hemming and his way of proceeding, I'm afraid. I think the situation is much different than in Hemming's day and as far as I'm concerned, I for one, shall keep on trying, at least, to improve this present code.

ROLLINS: I'm confident that the method of getting around this skewed opinion at the Congress used by the botanists is this. Every member of the congress has a vote, every attendee, but a fairly large block of votes

is assigned to institutions. For example, the New York Botannical Garden would have 10 votes, say, and the Berlin Botanical Garden, etc. The major taxonomic institutions throughout the world are assigned blocks of votes. And these can be cast by anyone present, or by proxy, or can be sent in without a representative present. This would keep a lop-sided congress from throwing out the code and doing something else.

SPEAKER: Yes, I've been aware of this. I didn't want to put it into my talk, but I'm glad it was brought out in the discussion. The only point I've wondered about, Dr. Rollings, is the assignment of these votes. Deciding who has 10 votes and who has 5 votes must be a really tough international diplomatic problem.

ROLLINS: It is, but it's done by country, with the consent of the people within the country. An attempt is made to assign these on the basis of the amount of taxonomic activity going on in the institution. If there are, say, 10 investigators in a place and they're actually productive, then they'd get 10 votes. This is rather arbitrary, and I agree with you that there are all kinds of difficulty. But it was done and it has not been objected to very profusely. There have been objections from some of the smaller countries, and there's always a certain amount of prestige value to having an institution represented with votes. This can be handled by assigning an institution a minimal vote, say 1 vote, as many of the small but active institutions are. But you also have obsolescence setting into different places, so that institutions which were once very strong have become weak. Then there has to be a downgrading of votes and this is objected to, but this is always done for a reason and can be justified.

SPEAKER: I can see difficulties in a lot of subjectivity involved here, but it still has impressed me that it is workable, and it certainly is an effort to achieve some representation of the botanists of the world and to avoid this possible domination by a local majority.

VOICE: Dr. Rollins, isn't there a controversy over who assigns the block of votes? Isn't there some sort of international section of plant taxonomy?

ROLLINS: Yes, there is. We are organized on an international basis. We work through the International Union of Biological Sciences, and then the International Association of Plant Taxonomy is the spark plug in keeping international opinion at a high level and allows people to air their opinions before the public, before they erupt into real controversy; it gives them a sounding board. There are difficulties there, too. Some people say that Taxon is a journal having to do only with nomenclature, and none of us like this. It certainly has a lot in there, but on the other hand it does give a forum for the world-wide botanical population to make their views known. Somebody has something to get off their chest, they publish it in Taxon and it can be taken into account or not.

STEYSKAL: I would simply like to make some comment on a branch of human knowledge that is only now attaining maturity and which I believe has a great deal to do with nomenclature. That is semantics. It is only within the last decade that things have been crystalizing in that study. The full value of the branch of knowledge called nomenclature really has a great deal to do with semantics. Because we taxonomists are in on the ground floor in the creation of names. If we propose a new name, we are doing something rather unique in the history of knowledge. The

name by its very basic meaning is a part of language and that brings up the subject of the meaning of the word like code. Here we have a good example of polysemy (?), as a semantic would say. A code, in one meaning of the word, is a body of rules. In another sense of the word, it is a different way of expressing the data or semantic content. The Morse code, like the Braille system of writing we may call a code and in that same context numerical names are a code rather than names. They are not properly parts of language.

Now, if in the future, we can adapt the study of semantics to our code in nomenclature, I think a great step forward can be made, but so far that is something to look forward to rather than to be made at the present time.

Another point in this same context are the two words transcription and transliteration. From a semantic standpoint, I think we have to maintain 2 distinct words there. I think the French would have to admit there are two words there given in their language. In any language those are learned words with two very distinct meanings, so even the French would have to admit both words.

SPEAKER: The French representatives on the editorial board have no difficulty; Transliteration is transcription for them.

VOICE: But to a linguist it's a different matter.

SPEAKER: There is no such work apparently. If there is it didn't come into the argument. The question is what did the word "transcription" in the definitive French text mean? And that meant transliteration. And of course this fits everything else in the code. All the opinions, the appendix to the old code, the directions for transliteration of Greek into Latin and so on,--everything fits. When you see that, we were wrong. Let's fact it.

I will assume that I do not need to go through the code article by article. There is no need reading or commenting on the fact that priority begins January 1, 1758, that Botanical and Zoologica Nomenclature are independent, etc. So I have picked some of the controversial areas, some of the difficult spots, concentrating on some of the weaknesses of the code, some comments on the frontier on code-making perhaps. Now I'm not sure that this necessarily will be useful to you in your teaching; it may, however, be useful background because I assume that if you teach nomenclature, you're going to be operating more advanced classes, and not beginning classes. How to teach the code is best left to the individual. There are various ways of approaching it.

Blackwelder has some interesting arrangements of the code. I'm thinking from the standpoint of presentation now as well as teaching, and his arrangement may very well be a good way to handle the code. That is, to bring together all the rules on generic names rather than taking them through availability, validity, homonomy, and so forth. The code was organized otherwise. Both ways are possible; both may have some advantages and disadvantages.

The committee tried to be as concise as possible, not repeating unduly; cross-referencing where it seemed essential in order to keep the thing just as short as possible, and short enough so perhaps it could be studied and digested as a whole. Blackwelder has criticised that

it's too complex. On page 402, for example, he says "The complexity of the code is now so great and so detailed that there is serious danger that taxonomists will not be able to use it effectively". This is a very damning statement. Yet opinions may differ. The arachnologist, Theodore Savory, in his little book, Naming the Living World, which some of you may have seen, says that "in its latest form the Code is a miracle of compression, a state that has followed the enunciation of guiding principles instead of separate attempts to deal individually with every puzzling detail. The wisdom of this is manifest".

Blackwelder says the Code is too complex, yet he himself seems to be more complex at times. I'm referring you to page 395 and his classification of names. Now there is some merit in his arrangement, but again it would increase the complexity and the size of the Code. And for example on page 389, "Any person doubting the actual complexity of the Code should examine Articles 21 and 22, on the Date of Publication." And yet a few pages later on page 399 he says, 'The 1961 Code has gone into considerable detail in specifying how the date of publication is to be determined. This is a helpful feature of the Code.' So in one case he says complexity is bad and in another case he says it is good, talking about the same thing.

I'm supposed to be reviewing the code, not Blackwelder's book. But it seemed to me that I couldn't escape reference to it. I got back from a several thousand mile trip a few days ago and found the book on my desk and immediately set to work to read it if not to study it. It is the only extensive and intensive critique of the code that has appeared. There have been many references to the code, Follett's review, a critique by Hobart Smith, numerous dabs here and there. But this is the only real extensive critique of the code that has appeared and it seemed to me particularly important to consider this, almost more important than to consider the Code itself in view of the extensive criticisms made.

TEACHING SYSTEMATICS

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Teaching is a subject of concern to everyone, in one way or another. I rarely find anyone who doesn't have an opinion on this subject. Today, I shall discuss some of the special problems of teaching systematics. Although some systematics is taught in every biological curriculum there are some unique aspects of the subject. There are exceptional opportunities for motivating students of all ages.

Blackwelder and others have argued that you don't need to teach systematics. It has been pointed out that most of the practicing systematists have never had a course on the subject. It could be argued that systematists are born, not made, and all we really do as teachers is to encourage them, and polish them. If we were to agree with this thought, the present discussion would be a waste of time. I do not believe this. In my opinion the most important single thing in teaching systematics is somehow to impart that enthusiasm for the field that motivates people.

This, of course, involves catching young people at the right time. There is a tremendous range here from youth through graduate students to senior citizens pursuing a hobby in retirement. There are many ways of reaching such people including school biology courses, science fairs, boy scouts, 4H clubs, etc. At all levels it is important not only to generate enthusiasm but also tp provide handbooks, field guides, junior museums, and other resources to help the beginner get into the subject. Some people regard the production of handbooks as a low level activity but I believe that it is one of the most important activities and, indeed, an obligation of the professional scientist.

Now to the college curriculum. As you know, there is a revolution going on in biological curricula. The trend is toward delaying treatment of the special fields for several years while concentrating on chemistry, physics, and mathematics. Essential though these subjects are, I favor spreading them through the curriculum so as to permit exposure to courses involving whole animals and populations and the elements of classification.

Assuming that we have a curriculum that is flexible enough to permit some teaching of non-molecular biology, what are the steps in the teaching of systematics? First, there is the so-called "service course" for non-majors. This is sometimes used to fill the breadth requirement. It is an excellent place to find and motivate students to careers in biology. Ordinarily, very little systematics is given at this level but a general classification has to be given with evolutionary concepts.

At the next level we have the introductory courses in the various groups of animals- protozoology, helminthology, entomology, ornithology, etc. Here, again, systematics usually is subordinate to other aspects of the subject such as anatomy, life histories, host relations, etc. However, the student is of necessity, introduced to the generally accepted classification of the group and learns to make identifications to whatever level is feasible in the group.

Beyond this, there are the special courses in taxonomic theory and practice given in most of the larger universities. In my opinion every

student in biology should have such a course to provide the background and point of view for whatever studies he may pursue in later years as a physiologist, ecologist, etc. I can think of no subject in biology that could not benefit by the comparative approach and by the concepts of population dynamics and evolution.

My method for teaching the "principles and practice" course has evolved over the years at Berkeley from a course given by Dr. E. C. VanDyke and later developed with my colleague, E. G. Linsley. The essence of the course is the laboratory "special problem". The student chooses or is assigned a group of specimens representing several genera and species. The object is to produce an actual taxonomic revision with keys, descriptions, synonymies, analyses of variation, maps of distribution, etc. At each stage lectures explain the steps such as literature search, species concepts, phylogenetic methods, and nomenclature. However, nomenclature is a subject that I have found can only be given in its most elementary form at this level. The new code is a small book and looks deceptively simple. Actually, it is so complicated that I have not succeeded in getting it across, even to graduate students in systematics, by means of lectures. I now believe that the only way to teach the intricacies of nomenclature is by assignment of special problems under a tutorial system.

The next aspect of the systematics teaching program, and the most important of all, is the research team of professor and student. As you know, in the English University system, taxonomic problems are not generally considered as appropriate for a Ph.D. In America er take the view that a problem in systematics may be just as challenging as any strictly experimental problem. The important point in any case is that there must be an intellectual challenge involving hypotheses to be advanced and tested by the scientific method. We do not give a Ph.D. for a pedestrian type thesis consisting only of descriptions and keys with no theoretical aspects or conclusions. We take the view that taxonomic theses should be publishable.

What qualities make for a good teacher? This question is as relevant in systematics as in other fields. And it is as difficult to answer. Traditionally, teacher evaluation has been done in American universities by colleagues or peers. However, in recent years students have assumed a role including the rating of professors and their courses. This is probably a healthy trend, though there is a danger of becoming involved in a popularity contest at the expense of the educational process. A more constructive and generally accepted method for obtaining the views of students is the "Teacher evaluation sheet", distributed at the end of a course and sent in unsigned to the professor to be used in any way that he sees fit. I have used such sheets for a number of years and have found them most helpful.

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